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The Structure and Functioning of Dryland Ecosystems – Conceptual Models to Inform the Vital-Sign Selection Process

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I. INTRODUCTION AND BACKGROUND

A. Purpose and Content of This Report

This report presents conceptual ecological models describing the structure and functioning of dryland ecosystems[1] of the Colorado Plateau and bordering ecoregions of North America. These models and the associated literature review have been prepared in support of the Southern Colorado Plateau Network (SCPN) of the National Park Service's Inventory and Monitoring Program (NPS I&M Program). As part of the I&M Program, the SCPN is tasked with the identification of "vital signs" for long-term monitoring in 19 NPS units located in the Colorado Plateau region of Utah, Arizona, Colorado, and New Mexico (Table 1). This report was developed to inform the consideration and selection of vital signs for dryland ecosystems in the SCPN. The SCPN and the Northern Colorado Plateau Network (NCPN – 16 NPS units) are working closely together to coordinate planning and implementation of their respective monitoring programs. As a consequence, this document also is intended to support the NCPN in the development of its monitoring plan and to facilitate the coordinated development of monitoring across both networks in the Colorado Plateau region.

This report begins with background information concerning vital signs, the intended purposes of conceptual models, and the geographical and ecological scope of the report. Following this background section, a general conceptual model and literature review are presented to characterize important functional relationships among biotic and abiotic components of dryland ecosystems. In the third section, several additional models are presented to describe particular patterns and processes of dryland ecosystem dynamics that have implications for ecosystem management and monitoring. Supplementary material is presented in accompanying appendices.

B. Vital Signs Definition

As defined by the NPS, vital signs are a subset of physical, chemical, and biological elements and processes of park ecosystems that are selected to represent the overall health or condition of park resources, known or hypothesized effects of stressors, or elements that have important human values. The elements and processes that are monitored are a subset of the total suite of natural resources that park managers are directed to preserve "unimpaired for future generations," including water, air, geological resources, plants and animals, and the various ecological, biological, and physical processes that act on those resources. Vital signs may occur at any level of organization including landscape, community, population, or genetic level, and may be compositional (referring to the variety of elements in the system), structural (referring to the organization or pattern of the system), or functional (referring to ecological processes) (from http://science.nature.nps.gov/im/monitor/vsm.htm#Definitions).

C. Purposes of Conceptual Models

In the vital-sign selection process, conceptual models are used to summarize existing knowledge and hypotheses concerning the structure and functioning of park ecosystems. An important goal of the models is to depict how natural drivers (e.g., climate) and anthropogenic stressors affect ecosystem structure and functioning. The ability of the monitoring program to detect the ecological effects of anthropogenic stressors is dependent upon interpreting trends in resource condition against the backdrop of intrinsic variation. Hypotheses concerning the effects of anthropogenic stressors on ecosystem structure and function must be grounded in an understanding of the relationship between natural drivers and the structure, functioning, and dynamics of ecosystems. Ecosystems and their components can be characterized on the basis of far more structural and functional attributes than can be monitored affordably. Thus another important goal of the models is to guide the identification of a parsimonious set of "information-rich" attributes that provides information concerning multiple aspects of ecosystem condition (Noon 2003).

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[1]An _ecosystem_ is a spatially explicit unit of the Earth that includes all of the organisms, along with all components of the abiotic environment within its boundaries (Likens 1992, cited by Christensen et al. 1996:670). _Ecosystem structure_ refers to the types, amounts, and spatial arrangement of biotic and abiotic components of an ecosystem. _Ecosystem functioning_ refers to the flow of energy and materials through the arrangement of biotic and abiotic components of an ecosystem (includes processes such as primary production, trophic transfer from plants to animals, nutrient cycling, water dynamics and heat transfer). In a broad sense, ecosystem functioning includes two components: ecosystem resource dynamics and ecosystem stability (Díaz and Cabido 2001).

Table 1. Selected characteristics of NPS units included in the Southern and Northern Colorado Plateau Networks. Ecoregion designations follow The Nature Conservancy and NatureServe (Groves et al. 2002), as modified from Bailey (1995).

Network / Park	Code	State	Size (ha)	Elevation (m)	Ecoregion
Southern Colorado Plateau Network					
Aztec Ruins National Monument	AZRU	NM	130	1705 - 1764	Colorado Plateau
Bandelier National Monument	BAND	NM	13,254	1626 - 3081	Southern Rocky Mts.
Canyon de Chelly National Monument	CACH	AZ	37,448	1687 - 2336	Colorado Plateau / Arizona-New Mexico Mts.
Chaco Culture National Historic Park	CHCU	NM	14,090	1832 - 2096	Colorado Plateau
El Malpais National Monument	ELMA	NM	46,559	1950 - 2554	Arizona-New Mexico Mts.
El Morro National Monument	ELMO	NM	518	2183 - 2304	Arizona-New Mexico Mts.
Glen Canyon National Recreation Area	GLCA	AZ/UT	505,868	930 - 2319	Colorado Plateau
Grand Canyon National Park	GRCA	AZ	493,050	348 - 2798	Colorado Plateau
Hubbell Trading Post National Historic Site	HUTR	AZ	65	1920 - 1946	Colorado Plateau
Mesa Verde National Park	MEVE	CO	21,093	1833 – 2613	Colorado Plateau
Navajo National Monument	NAVA	AZ	146	1658 - 2294	Colorado Plateau
Petrified Forest National Park	PEFO	AZ	38,024	1618 - 1891	Colorado Plateau
Petroglyph National Monument	PETR	NM	2,915	1519 - 1838	Arizona-New Mexico Mts.
Rainbow Bridge National Monument	RABR	UT	65	1129 - 1492	Colorado Plateau
Salinas Pueblo Missions National Monument	SAPU	NM	433	1815 - 2058	Arizona-New Mexico Mts.
Sunset Crater Volcano National Monument	SUCR	AZ	1,227	2076 - 2441	Arizona-New Mexico Mts.
Walnut Canyon National Monument	WACA	AZ	1,456	1896 - 2106	Arizona-New Mexico Mts.
Wupatki National Monument	WUPA	AZ	14,350	1304 - 1744	Colorado Plateau
Yucca House National Monument	YUHO	CO	14	1767 - 1805	Colorado Plateau
		TOTAL	**1,189,205**		
Northern Colorado Plateau Network					
Arches National Park	ARCH	UT	30,966	1206 - 1725	Colorado Plateau
Black Canyon of the Gunnison National Park	BLCA	CO	12,159	1636 - 2752	Southern Rocky Mts.
Bryce Canyon National Park	BRCA	UT	14,502	2000 - 2777	Utah High Plateaus
Canyonlands National Park	CANY	UT	136,610	1140 - 2189	Colorado Plateau
Capitol Reef National Park	CARE	UT	97,895	1182 - 2730	Colorado Plateau
Cedar Breaks National Monument	CEBR	UT	2,491	2461 - 3247	Utah High Plateaus
Colorado National Monument	COLM	CO	8,310	1411 - 2160	Colorado Plateau
Curecanti National Recreation Area	CURE	CO	17,433	1982 - 2898	Southern Rocky Mts.
Dinosaur National Monument	DINO	CO/UT	85,097	1442 - 2747	Utah-Wyoming Rocky Mts.
Fossil Butte National Monument	FOBU	WY	3,318	2012 - 2466	Wyoming Basins
Golden Spike National Historic Site	GOSP	UT	1,107	1317 - 1613	Great Basin
Hovenweep National Monument	HOVE	CO/UT	318	1548 - 2056	Colorado Plateau
Natural Bridges National Monument	NABR	UT	3,009	1702 - 2019	Colorado Plateau
Pipe Spring National Monument	PISP	AZ	16	1495 - 1559	Colorado Plateau
Timpanogos Cave National Monument	TICA	UT	101	1669 - 2452	Utah-Wyoming Rocky Mts.
Zion National Park	ZION	UT	59,900	1112 - 2661	Colorado Plateau
		TOTAL	**474,709**		

No single conceptual model can satisfy all needs. Spatially explicit applications such as ecological resource assessments, monitoring design, and landscape-level ecological modeling ultimately require site-specific models, but the monitoring program also requires generalized ecological models to facilitate communication among scientists, managers, and the public regarding ecosystems and how they are affected by human activities and natural processes. Together, the NPS and USGS have adopted an iterative approach of first developing general conceptual models for broadly defined ecosystem types, and then adapting and refining those models with site-specific data concerning abiotic constraints, land-use history, current condition, and specific patterns of ecosystem dynamics. Models presented in this report necessarily are very generalized because of the great diversity of dryland ecosystems found in SCPN and NCPN parks.

Previous NPS reports established a framework for the conceptual modeling effort associated with the NCPN and SCPN monitoring programs (see Evenden et al. 2002, Thomas et al. 2003, Miller et al. 2003). The overall conceptual framework presented in these earlier documents provides a basis for the material included in this report, but it is not repeated here in detail.

D. Geographical and Ecological Scope

Given the distribution of parks included in the NCPN and SCPN, the geographic scope of this report extends from northern Utah and southwestern Wyoming southward to north-central Arizona and New Mexico (Fig. 1). This region is centered on the Colorado Plateau physiographic province, but region also includes portions of the Wyoming Basin, the Southern and Central Rocky Mountains, and the Basin and Range physiographic provinces (Hunt 1974). Park elevations range from 348 m at the lower end of the Colorado River corridor in GRCA to 3247 m at CEBR in southwestern Utah (Table 1). [Four-letter codes for park names will be used throughout this report. Table 1 provides a key.] Mean annual precipitation (MAP) at National Weather Service Cooperative Network (NWS) stations located in or near NCPN and SCPN parks ranges from 162 mm at Page, Arizona (GLCA), to 752 mm at CEBR (Fig. 1). Because this report focuses on characteristics of dryland ecosystems, it is generally restricted to those areas where MAP is less than 450 mm – the upper limit for piñon-juniper vegetation (pygmy woodlands and forests dominated by *Pinus edulis* and *Juniperus osteosperma*) at MEVE (Floyd et al. 2003a). With the exception of the dry, high-elevation Gunnison Basin (CURE), areas receiving less than 450 mm in this region are generally found below 2100-2300 m. Approximately 90-95 percent of NCPN park lands and 85-90 percent of SCPN park lands fall below these precipitation and elevation zones (estimated from data presented by Evenden et al. 2002 and Thomas et al. 2003). [See reports by Evenden and colleagues (2002) and Thomas and colleagues (2003) for additional park-specific information.]

Dryland ecosystems within the scope of this report are characterized by mixtures of pygmy conifers (*Juniperus* and *Pinus* spp.), shrubs, dwarf shrubs, herbaceous plants, and biological soil crusts. Excluded from this report are montane shrublands (or "petran chaparral") that typically occur above the piñon-juniper zone.

Across the geographic region included in the report, there is tremendous diversity in the composition, structure, and functioning of dryland ecosystems. This diversity is attributable to regional- and local-scale variations in climate, landforms, soils, and land-use history. Variations in biogeographic history are reflected in the fact that the region also encompasses several distinct floristic areas (McLaughlin 1986, 1989). As a consequence of these factors, SCPN and NCPN parks are found in seven broadly-defined ecoregions (Table 1, Fig. 2).

Numerous schemes have been used to classify ecosystems and plant communities of the region (e.g., Küchler 1964, Brown 1982, Dick-Peddie 1993, Spence et al. 1995). These schemes are based on various combinations of floristic, physiognomic, topographic and climatic parameters (Spence et al. 1995). Because this report focuses on ecosystem structure and function, it adopts a functional approach that generally corresponds with physiognomy rather than a particular classification scheme.
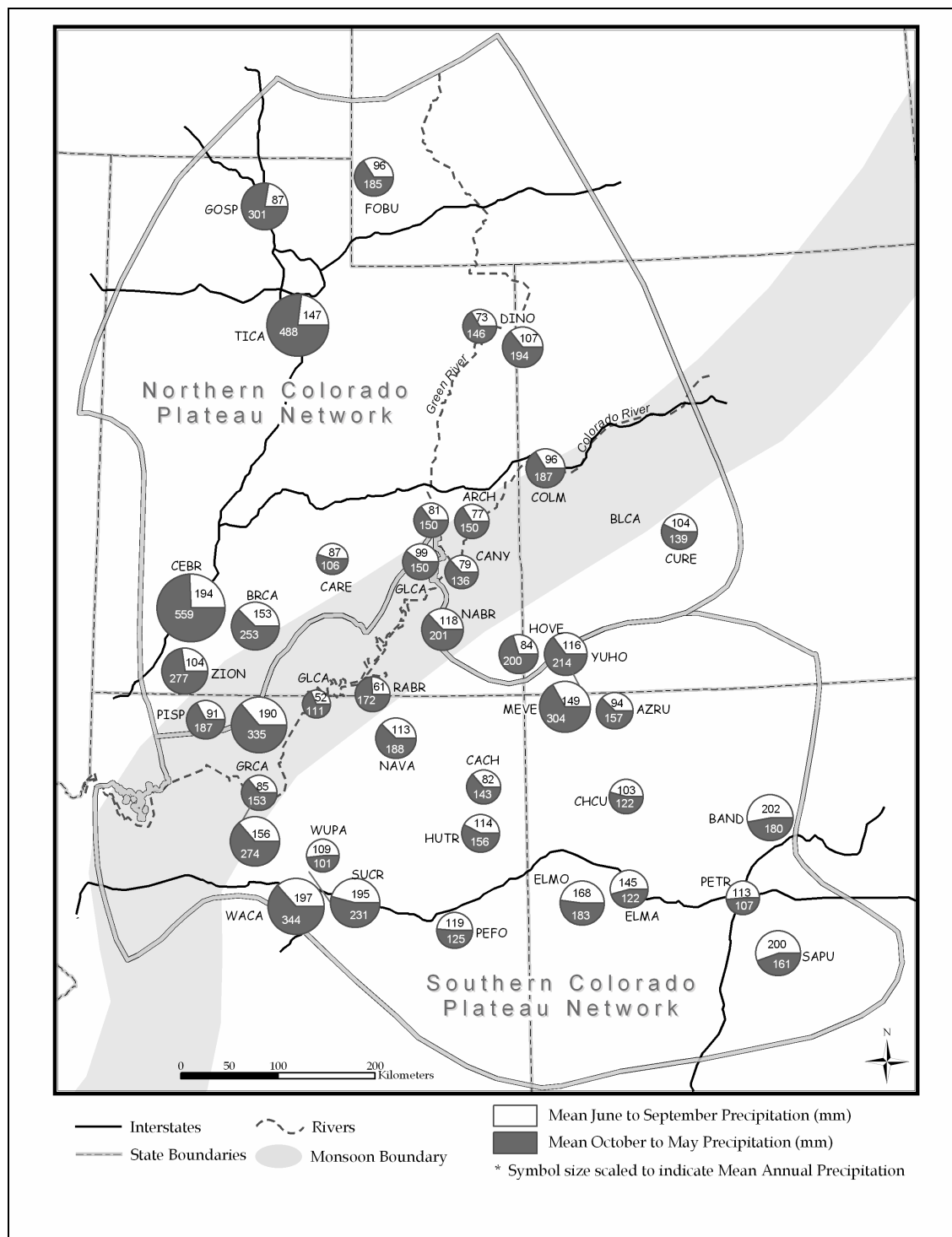
Figure 1. Map showing mean annual precipitation (symbol diameter) and mean seasonal precipitation (symbol segments) for National Weather Service Cooperative Network stations located at or near NPS units of the Southern and Northern Colorado Plateau Networks. Shaded zone approximates the mean northwestern extent of summer monsoon moisture (from Mitchell 1976). Precipitation data were acquired from the Western Regional Climate Center (http://www.wrcc.dri.edu/climsum.html). See Table 1 for key to four-letter park codes.
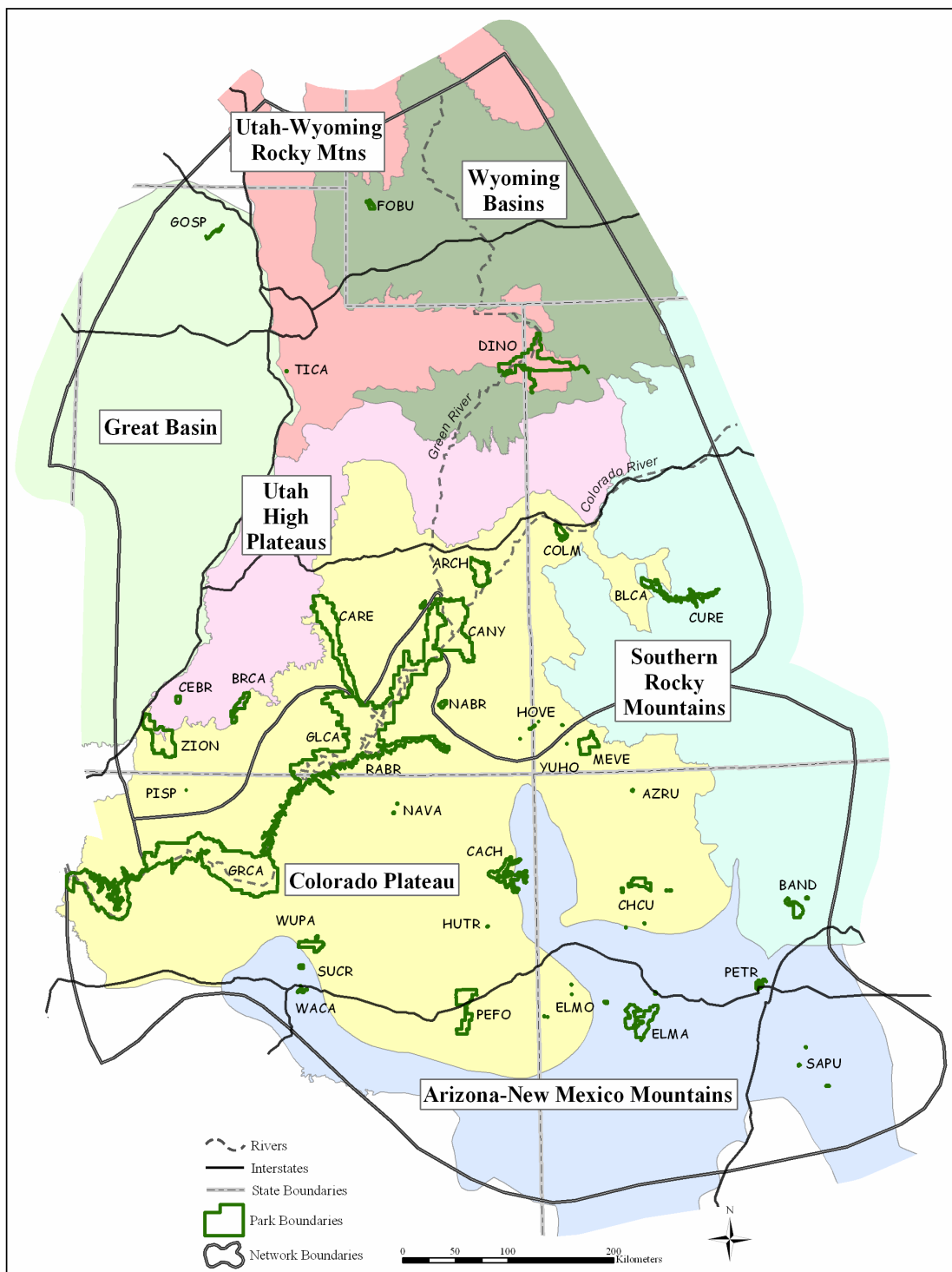
Figure 2. Map showing location of NCPN and SCPN parks in relation to ecoregions. Ecoregion designations follow The Nature Conservancy and NatureServe (Groves et al. 2002), as modified from Bailey (1995). See Table 1 for key to four-letter park codes.

II. STRUCTURE AND FUNCTIONAL RELATIONSHIPS

This section begins with a brief overview of the ecosystem framework adopted by the SCPN and NCPN. Following this overview, a general conceptual model and literature review are presented to characterize important functional relationships among biotic and abiotic components of dryland ecosystems.

A. Background: The Jenny-Chapin Model of Ecosystem Sustainability

Jenny (1941, 1980) proposed that soil and ecosystem processes are determined by five *state factors* – climate, organisms, relief (topography), parent material, and time since disturbance. Jenny's state-factor approach has been widely applied as a framework for examining temporal and spatial variations in ecosystem structure and function (e.g., Walker and Chapin 1987, Vitousek 1994, Seastedt 2001). Chapin and colleagues (1996) recently extended this framework to develop a set of ecological principles concerning ecosystem sustainability. They defined "...a sustainable ecosystem as one that, over the normal cycle of disturbance events, maintains its characteristic diversity of major functional groups, productivity, and rates of biogeochemical cycling" (Chapin et al. 1996:1016). These ecosystem characteristics are determined by a set of four "interactive controls" – climate, soil-resource supply, major functional groups[2] of organisms, and disturbance regime – and these interactive controls both govern and respond to ecosystem attributes. Interactive controls are constrained by the five state factors, which determine the "constraints of place" (Dale et al. 2000). The SCPN and NCPN have adopted a modified version of the Jenny-Chapin model as a general ecosystem framework for guiding the development of additional conceptual models and the consideration of vital signs (Fig. 3).
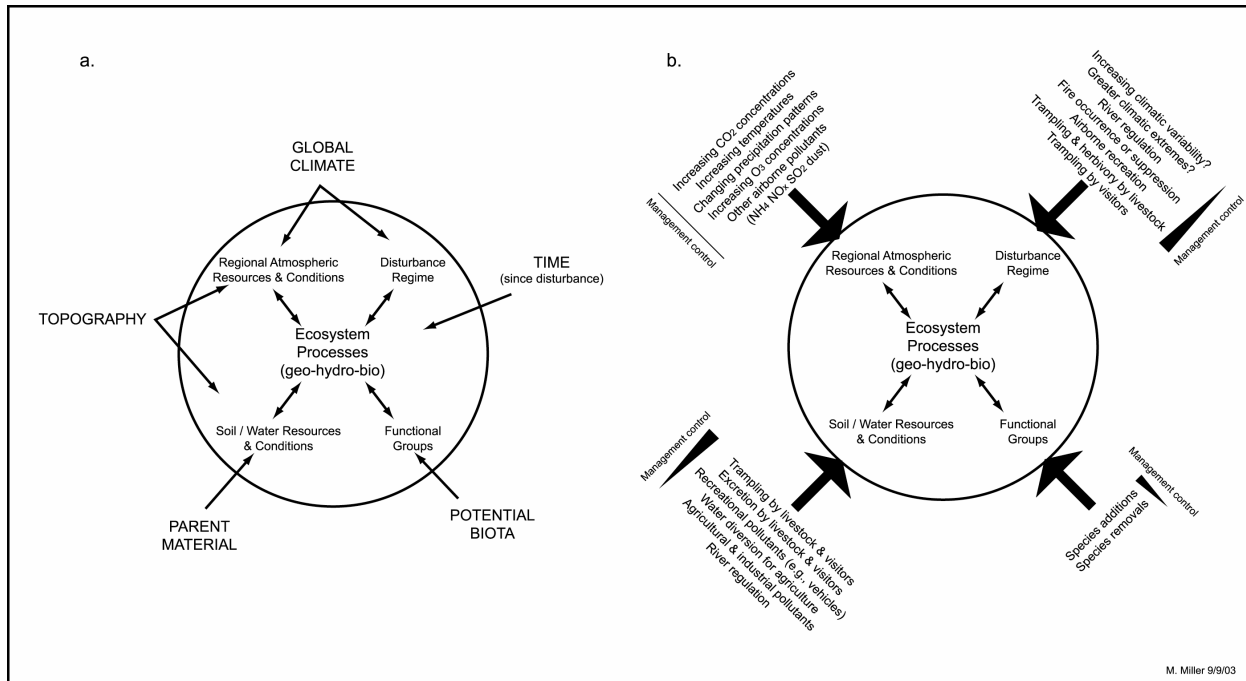
Figure 3. Modified version (a) of the Jenny-Chapin model that serves as the general ecosystem model for the SCPN and NCPN, and (b) the array of stressors affecting SCPN/NCPN ecosystems arranged in the model in relation to their first-order effects. Complex, higher order effects occur as the four major controls interact via ecosystem processes. The circle represents the boundary of the ecosystem.

For vital-signs monitoring, a key aspect of the interactive-control model is the associated hypothesis that interactive controls must be conserved for an ecosystem to be sustained. Large changes in any of the four interactive controls are predicted to result in a new ecosystem with different characteristics than the original system (Chapin et al. 1996). For example, major changes in soil resources (e.g., through erosion or other

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[2] *Functional groups* are groups of species that have similar effects on ecosystem processes (Chapin et al. 1996). This concept is generally synonymous with *functional types*.

mechanisms) can greatly affect productivity, recruitment opportunities, and competitive relations of plants, and thus can cause significant changes to the structure and functioning of plant communities and higher trophic levels. Changes in vegetation structure can affect the ecosystem's disturbance regime through altered fuel characteristics. These factors and processes in combination can result in an altered system which is fundamentally different from the original system in terms of structure, functioning, and dynamics.

B. General Model

Expanding on the framework of the Jenny-Chapin model, Fig. 4 serves as a general conceptual model describing structural components and functional relationships that characterize dryland ecosystems. Climatic and atmospheric conditions, soil resources, major functional groups, and disturbance regimes characteristic of dryland ecosystems are reviewed in this section. (Appendix A provides a tabular supplement to Fig. 4.)

1. Regional Climatic and Atmospheric Conditions

a. Precipitation Regime

Precipitation regime is the most important climatic factor defining the characteristics of dryland ecosystems because of the importance of precipitation inputs for driving water-limited ecological processes such as primary production, nutrient cycling, and plant reproduction (Noy-Meir 1973, Comstock and Ehleringer 1992, Whitford 2002). Precipitation seasonality (i.e., timing in relation to the annual cycle of potential evapotranspiration) is a particularly important attribute because it strongly controls the partitioning of precipitation among various compartments of the hydrologic budget – evaporation, transpiration, runoff, drainage, and soil-water storage. Because of its effects on hydrologic partitioning, precipitation seasonality is a major determinant of ecosystem dominance by different vegetative life forms and functional groups (Comstock and Ehleringer 1992).

In the area encompassed by this report, precipitation seasonality varies regionally due to the influence of the Arizona monsoon (Mitchell 1976, Peterson 1994). The Arizona monsoon (also referred to as the "southwest monsoon" or the "Mexican monsoon") is recognized by climatologists as the northernmost portion of an extensive summer monsoon region that extends to central Mexico and the western slopes of the Sierra Madre Occidental (Higgins et al. 1998). Areas affected by monsoon circulation receive greater amounts of summer precipitation from moist air masses derived from the gulfs of Mexico and California. Notably, the mean northwestern extent of summer monsoon moisture is approximated by a band which cuts across the Colorado Plateau (Fig. 1). Areas that occur well northwest of this band are dominated by cool-season precipitation (e.g., GOSP, TICA, FOBU), whereas areas that occur southeast of this band (e.g., BAND, ELMA, SAPU) receive higher amounts of summer monsoon precipitation from convective thunderstorms. Areas close to the band are generally characterized by a bimodal precipitation regime, with summer monsoon precipitation that is highly variable from year to year.

Ehleringer and colleagues (2000) hypothesized that effects of global change on atmospheric circulation patterns and precipitation may be seen relatively early in the Colorado Plateau region because of the presence of this significant climatic boundary. In an analysis of regional precipitation trends for the central Colorado Plateau, Spence (2001) found that there has been a weak trend towards increasing winter precipitation but no evidence for significant changes in monsoon precipitation patterns since the 1960's. Annual minimum temperatures were found to have increased significantly across the region during the same time period (Spence 2001).

Regional precipitation patterns are affected by global-scale fluctuations in sea-surface temperatures, atmospheric pressure, and atmospheric circulation patterns that vary at two different time scales (Hereford et al. 2002). Short-term interannual variations in precipitation are related in part to the occurrence of El Niño and La Niña conditions – the two contrasting phases of the El Niño – Southern Oscillation (ENSO) phenomenon that is driven by variations in sea-surface temperatures in the eastern tropical Pacific Ocean (Hereford and Webb 1992, Cayan et al. 1999, Hereford et al. 2002). Hereford and colleagues (2002) recently reported their analyses of 20th century precipitation patterns on the Colorado Plateau in relation to ENSO phases. They found that the detailed relationships were complex, but that strong El Niño episodes generally increased the variability of warm-season precipitation or the frequency of above-normal cool-

season precipitation. In contrast, strong La Niña episodes tended to cause normal, low-variability warm-season precipitation and below-normal cool-season precipitation. Whether characterized by dry or wet conditions, extreme years can have long-lasting consequences for ecosystem structure and functioning by causing episodes of plant mortality or establishment (Ehleringer et al. 2000).

 Decadal-scale variations in precipitation patterns are related to a recently recognized phenomenon known as the Pacific Decadal Oscillation, or PDO (Mantua and Hare 2002, Hereford et al. 2002). Precipitation variability associated with the PDO is partly related to cyclical variations in sea-surface temperatures in the northern Pacific Ocean, although mechanisms driving PDO variability remain poorly understood (Mantua and Hare 2002). In their analyses of 20th-century precipitation patterns on the Colorado Plateau, Hereford and colleagues (2002) found evidence for three relatively distinct precipitation regimes that appeared to be in phase with the PDO. The first of these was a period of relatively wet conditions from 1905 to 1941. Notably, the onset of this wet period corresponds well with the pulse of ponderosa pine establishment that was documented throughout much of the Southwest during the first decade of this century (Cooper 1960, Savage 1991). Following this wet period, two other distinctly recognizable precipitation regimes occurred from 1942 to 1977 (dry) and from 1978 to 1998 (wet). The marked shift to dry conditions that began in 1999 and continues through the present suggests a transition to the dry PDO phase that could continue for the next 2-3 decades (Hereford et al. 2002). This has important implications for ecosystem management[3] and monitoring in the region due to the effects of precipitation patterns on disturbance regimes (Swetnam and Betancourt 1998) and on the capacity of ecosystems to resist or recover from natural disturbances and human land-use activities (Ehleringer et al. 2000, Whitford 2002).

In addition to temporal variability, spatial variability is another defining attribute of dryland precipitation regimes (Noy-Meir 1973, Whitford 2002). Topography and storm type are two factors that control spatial variability in precipitation. On a local scale, precipitation tends to increase with increasing elevation due to orographic effects of topography (precipitation caused by adiabatic cooling of rising air masses), but rain shadows also can develop on the lee side of massive topographic features. Such rain-shadow effects can produce high-elevation zones of aridity like the Gunnison Basin in western Colorado. As for storm type, summer precipitation derived from convective thunderstorms is characterized by greater spatial variability than winter precipitation from frontal storms (Noy-Meir 1973, Whitford 2002).

The size of precipitation events also is an important attribute of dryland precipitation regimes (Noy-Meir 1973, Sala and Lauenroth 1982, Lauenroth and Sala 1992, Ehleringer et al. 2000, Whitford 2002, Austin et al. *in press*, Loik et al. *in press*). Event size and timing (seasonal, diurnal, and in relation to antecedent environmental conditions) in combination are important for determining ecological responses to precipitation due to effects on hydrologic partitioning. A significant characteristic of dryland precipitation regimes is the predominance of small events (e.g., Fig. 5). Depending on environmental conditions, small events (< 5mm) may trigger soil-surface processes such as nutrient mineralization / volatilization, whereas larger events may be required to initiate seed germination, plant physiological processes such as photosynthesis, and hydrologic processes such as soil-water recharge (Ehleringer et al. 2000). The capacity to respond to precipitation events of different sizes and timing is an important ecophysiological characteristic of plants that determines their ability to persist under particular precipitation regimes (Sala and Lauenroth 1982, Ehleringer et al. 2000).

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[3] *Ecosystem management* is the process of land-use decision making and land-management practice that takes into account the full suite of organisms and processes that characterize and comprise the ecosystem and is based on the best understanding currently available as to how the ecosystem works. Ecosystem management includes a primary goal of sustainability of ecosystem structure and function, recognition that ecosystems are spatially and temporally dynamic, and acceptance of the dictum that ecosystem function depends on ecosystem structure and diversity (Dale et al. 2000:642).

M. Miller & L. Thomas, Jan. 2004
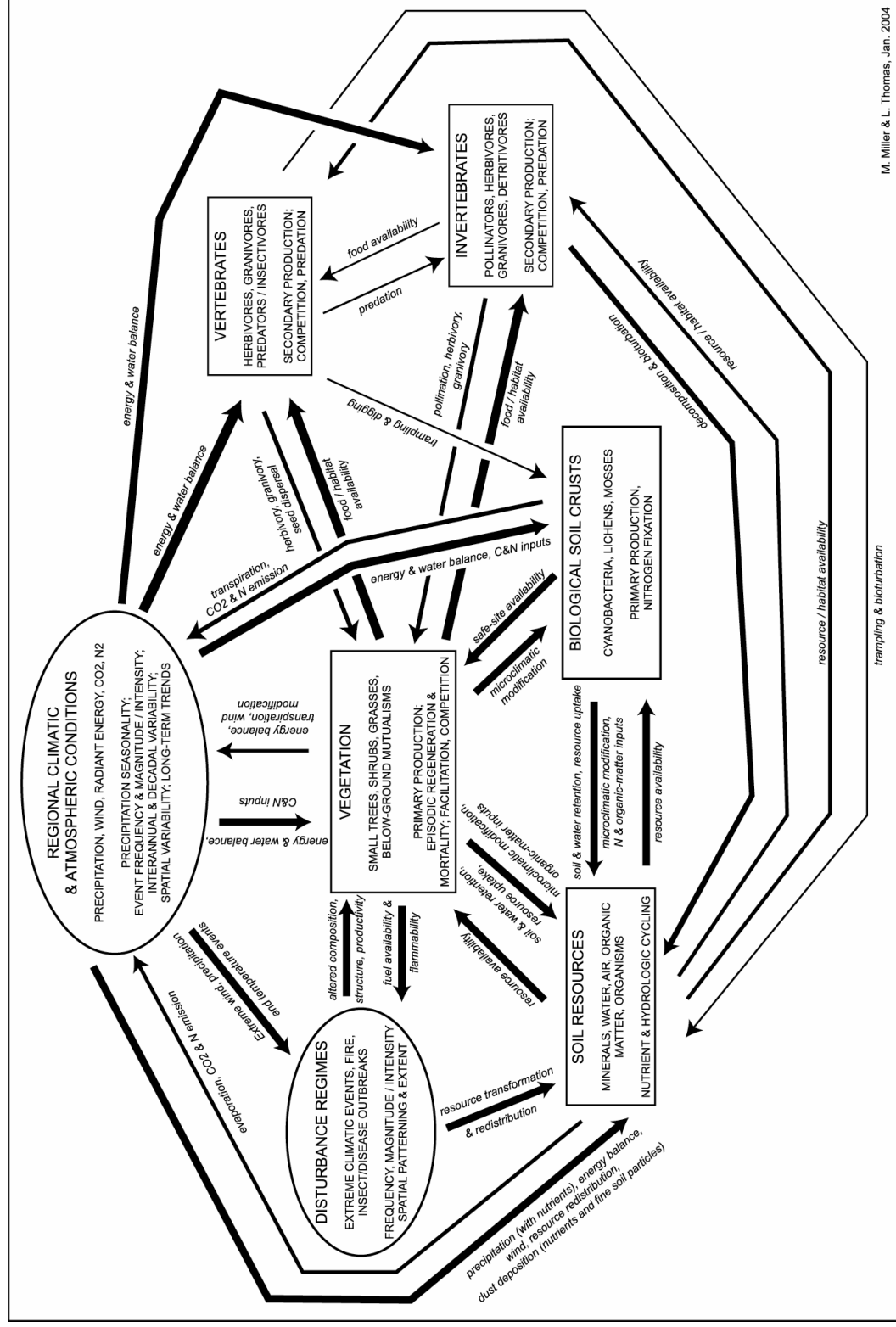
Figure 4. General conceptual model depicting the structure and functioning of dryland ecosystems. Ovals indicate major drivers of ecosystem change and temporal variability, as well as important attributes of drivers. Boxes indicate major structural components and important processes. Arrows indicate functional relationships among components, and line weights indicate relative importance of relationships. The model is constrained by global climatic and atmospheric conditions, topography, parent material, potential biota, and time.
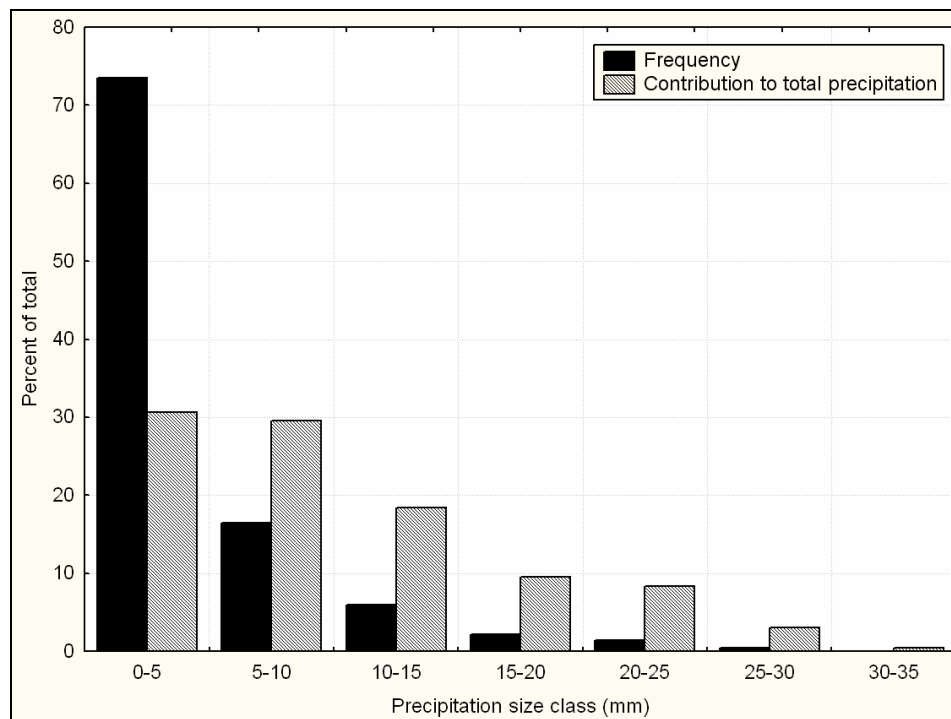
Figure 5. Distribution of precipitation events (based on daily values) by size class at the Needles District of Canyonlands National Park, 1965-1998.

Precipitation intensity (amount per unit time period) also affects hydrologic partitioning of precipitation. Precipitation intensity, soil characteristics (e.g., texture and antecedent moisture conditions), and soil-surface features (e.g., soil-surface roughness; amount, type, and distribution of ground cover) together determine whether precipitation events result in infiltration or runoff (Whitford 2002, Breshears et al. 2003). If precipitation intensity exceeds the soil infiltration rate, runoff will be generated – increasing the potential for soil erosion. In the Colorado Plateau region, precipitation intensity tends to increase with increasing elevation and decreasing latitude (Fig. 6) because these variables together generally indicate relative exposure to high-intensity convective thunderstorms. Approximately 66 percent of the variation in precipitation intensity across the region can be explained by elevation and latitude.

Studies conducted in some dryland ecosystems have found time lags in the response of above-ground net primary production (ANPP) to interannual variations in precipitation (e.g., Lauenroth and Sala 1992, Oesterheld et al. 2001, Wiegand et al. 2004). For example, analyses of a 52-year data set from a short-grass steppe ecosystem in Colorado found that only 39 percent of the interannual variation in ANPP could be explained by current-year precipitation (Lauenroth and Sala 1992). The best model, which accounted for 60 percent of ANPP variability, included precipitation from the current year *and* from the two previous years (Oesterheld et al. 2001). Due to this lag or carryover effect, ANPP fluctuations are buffered if wet and dry years alternate but amplified if multi-year sequences of dry and wet years occur (Oesterheld et al. 2001, Wiegand et al. 2004). Preliminary analyses of monitoring data from CANY suggest that production-precipitation lags also may occur in Colorado Plateau systems (Belnap unpubl.).
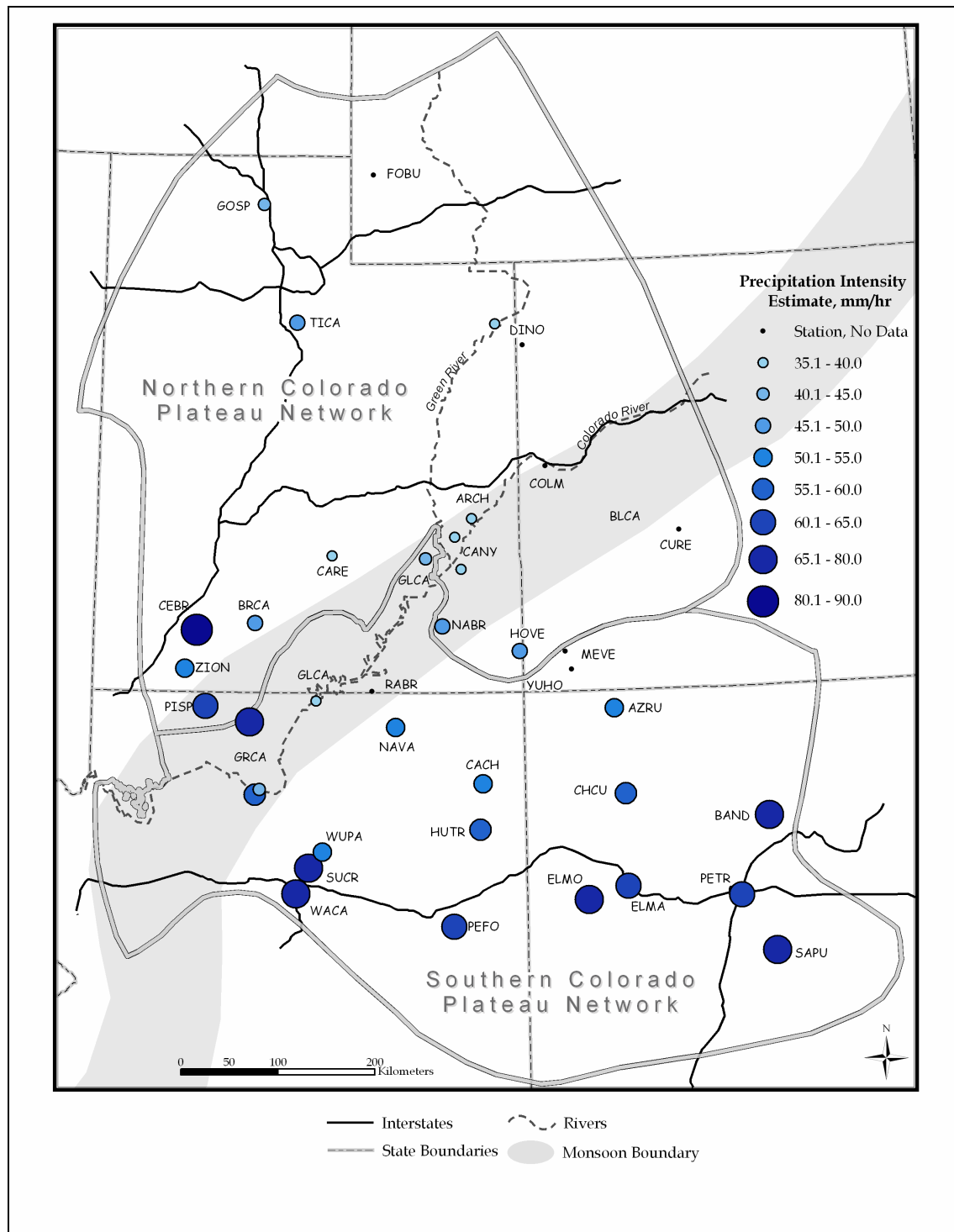
Figure 6. Map depicting regional variations in the estimated maximum intensity of precipitation (mm/hr) that can be expected to occur over a 5-min period with 50 percent probability during any given year at NWS stations located at or near NCPN and SCPN units. Shaded zone approximates the mean northwestern extent of summer monsoon moisture (from Mitchell 1976). Data were acquired from NOAA's Precipitation Frequency Data Server (http://hdsc.nws.noaa.gov/hdsc/pfds/). See Table 1 for key to four-letter park codes.

b. Wind

Wind is another atmospheric phenomenon that can have important effects on the structure and functioning of dryland ecosystems. As a driver of near-surface air circulation, wind strongly affects evapotranspiration rates and thus can modify the energy and water balances of plants and soils (Larcher 1995). Like precipitation, wind also is an important force driving the redistribution of soil resources both within and among ecosystems (Whicker et al. 2002). In a recent comparison of wind- and water-driven erosion in dryland ecosystems, Breshears and colleagues (2003) estimated that wind erosion exceeded water erosion by about 33 times at a shrubland site and by about five times at a forest site. At a grassland site, the authors estimated that water erosion was about three times greater than wind erosion. Soil texture, vegetation structure, and ground cover were important variables affecting among-site differences in the relative importance of wind and water erosion. The frequency-intensity distributions of erosion-driving wind and precipitation events are climatic factors that also affect the importance of wind versus water erosion on particular sites (Breshears et al. 2003). Finally, wind also interacts with topography to influence fire behaviour.

2. Soil Resources

a. Inherent Edaphic Heterogeneity

Soil resources, including mineral nutrients, organic matter (including litter), water, and soil biota, are fundamental determinants of ecosystem structure and function (Jenny 1980, Vitousek 1994, Reynolds et al. 2003). A characteristic feature of soils in the Colorado Plateau region is tremendous spatial heterogeneity attributable to combined effects of geology, topography and geomorphic processes (Brotherson et al. 1985, Norton et al. 2003). Due to low rates of weathering and pedogenic processes in dryland environments, the relative importance of parent material as a factor determining soil properties generally increases with aridity (Jenny 1941). Geologic and climatic features of the Colorado Plateau have produced weakly developed soils with physical and chemical characteristics that closely match the shales, sandstones, limestones, and igneous materials from which they derived. Geomorphic processes such as erosion and deposition have built upon this geologic template to generate mosaic landscapes composed of soil patches differentiated on the basis of depth, particle-size distributions, mineralogy, and degree of profile development. Effects of human activities (Amundson and Jenny 1991) and aeolian dust inputs (Reynolds et al. 2001) are superimposed on this mosaic. Whereas disturbances such as fire often are the primary factors responsible for generating landscape patterns in comparatively mesic environments (Clark 1991), inherent edaphic heterogeneity is a primary cause of landscape patterns in dryland portions of the Colorado Plateau region.

b. Soil Functions and Soil Quality

Soils perform several ecological functions pertinent to ecosystem management and monitoring. Soils regulate hydrologic processes and the cycling of mineral nutrients. As the medium for storage and delivery of water and nutrients, soils also sustain the existence and productivity of plant and animal populations. The capacity of a specific kind of soil to perform these functions is described by the concept of *soil quality* (Karlen et al. 1997, Herrick et al. 2002, Norfleet et al. 2003). Soil quality and soil functioning are determined by inherent soil properties such as texture, depth, and mineralogy; and by dynamic soil properties such as organic-matter content, aggregate stability, soil-surface roughness, and structure (Seybold et al. 1999). Relative to inherent properties, dynamic properties are more subject to change under the influence of climatic fluctuations, land-use activities, natural disturbances, and management actions. Severe soil degradation (i.e., erosion) can result in the persistent alteration of inherent soil properties such as depth and texture.

Within a given climatic region, soil is the most important factor affecting the structure of terrestrial ecosystems because of its role in mediating the bioavailability of water and mineral nutrients (Whitford 2002). This is particularly true of dryland ecosystems because small differences in soil physical and chemical traits can have relatively large effects on water and nutrient bioavailability (Comstock and Ehleringer 1992, McAuliffe 2003).

c. Resource Limitations

In general, water has been described as the soil resource that most commonly limits the productivity of dryland ecosystems (Noy-Meir 1973, Ehleringer et al. 2000). But there is increasing recognition that

nutrients also can limit dryland productivity, particularly during periods when water is abundant relative to evapotranspirational demands (Havstad et al. 2000, Archer and Bowman 2002, Whitford 2002). Water and nutrient uptake are not independent (Barber 1995, Marschner 1995), and Chapin (1991) has argued that that the effects of low soil moisture on nutrient availability to plants may be as significant as the direct effects of water stress on plant performance. Following a review of fertilization experiments in dryland ecosystems, Hooper and Johnson (1999) concluded that there was no evidence for a shift from water to nutrient limitation along a geographic gradient of increasing water availability. Instead, their review supported the hypothesis that water and nitrogen (N) generally are co-limiting in dryland ecosystems. In addition to N, field studies on the Colorado Plateau suggest important roles for phosphorus (Miller et al. 2001, Neff unpubl.) and potassium (Belnap and Phillips 2001) in structuring dryland ecosystems of the region.

The retention of limiting water and nutrient resources is essential for sustaining the structure and functioning of dryland ecosystems (Ludwig and Tongway 1997, 2000; Whitford 2002). Dynamic soil properties important for water and nutrient retention include soil structure, infiltration capacity, soil-surface roughness, organic-matter content, soil aggregate stability, and soil biotic activity (Herrick et al. 2002). Other ecosystem components that promote the capture and retention of soil resources include vegetation, biological soil crusts, and other soil-stabilizing features such as litter and rocks (Warren 2001, Whitford 2002).

d. Spatial Patterning

Coupled spatial patterning of vegetation and soil resources is a common characteristic of dryland ecosystems due to strong interactions between plants and soils (Charley and West 1975; Schlesinger et al. 1990, 1996). Vegetation affects the spatial distribution of soil resources due to processes such as nutrient uptake, above- and below-ground litter deposition, and microclimatic modification, and due to interactions of vegetation with air- and wind-driven processes of erosion and deposition (Whitford 2002). Vegetation patterns also are strongly influenced by spatial patterns of resource availability, resulting in a classic positive-feedback relationship (Aguiar and Sala 1999). Because the spatial patterning of soil resources is so closely linked with several important biotic and abiotic processes, changes in resource distributions both within (canopy vs. interspace) and among ecosystems can indicate significant changes in ecosystem functioning (Ludwig and Tongway 1997, 2000). Some workers have suggested that indices of soil-resource patterning may prove useful as early-warning indicators of ecosystem degradation in dryland environments (Herrick and Whitford 1995, Havstad et al. 2000).

3. Major Functional Groups

a. Background

Chapin and colleagues (1996) identified biotic functional groups (hereafter described as _functional types_) as one of the four interactive controls of ecosystem sustainability because of the capacity of dominant functional types to shape the structure and functioning of whole ecosystems. Associated with efforts to model ecological consequences of global change, a vast literature has developed concerning different approaches to deriving or classifying functional types – particularly with respect to vegetation (e.g., Smith et al. 1997). Identification and use of a particular functional-type scheme depends on the ecosystem function(s) of interest. Several workers have proposed that the most important functions in dryland ecosystems are those that control the retention of water and nutrient resources because productivity and diversity cannot be sustained in systems that fail to retain resources (Ludwig and Tongway 1997, Whisenant 1999, Whitford 2002). Functions affecting the cycling and retention of water and nutrient resources will be emphasized here, but other functions will not be excluded. For purposes of this report, it is less important to adopt a specific functional-type classification scheme than it is to take a broad functional perspective when considering the biotic components of dryland ecosystems.

Without adopting a particular classification scheme, it remains useful to identify two general categories of functional types that are equally important for ecosystem dynamics. These are (1) _functional effect types_ – organisms with similar effects on ecosystem functions such as primary production, nutrient cycling, and soil stabilization, and (2) _functional response types_ – organisms with similar responses to environmental factors such as climate, resource availability, natural disturbances, and land-use activities (Walker 1997, Walker et al. 1999, Díaz and Cabido 2001, Díaz et al. 2002). The distinction between these two types is important for

considering how biotic composition affects the resistance and resilience[4] of ecosystems to climatic fluctuations and changes, natural disturbances, and anthropogenic stressors (Walker et al. 1999). Although some workers have emphasized the importance of overall functional diversity for sustaining ecosystem processes (Tilman et al. 1997), the effect-response distinction suggests that long-term ecosystem functioning may be favored when different functional response types are nested within the same functional effect type (Walker et al. 1999, Díaz and Cabido 2001). Thus functional redundancy and functional diversity both may be important for long-term persistence of ecosystem structure and function.

b. Vegetation

At a broad level, vegetation generally is recognized as *the* dominant functional type in terrestrial ecosystems. In addition to conducting photosynthesis, aboveground structures of vascular plants protect soils from erosive raindrops, obstruct erosive wind and overland water flow, and enhance the capture and retention of soil resources. Litter from plants further reduces the erosive impacts of rainfall on soil surfaces and provides inputs to soil organic matter for nutrient cycling. Aboveground structures of plants also modify the physical environment by shading and litter deposition, strongly affecting spatial and temporal patterns of soil-resource availability to other organisms. Roots stabilize soils, are conduits for resource acquisition and redistribution, and provide organic-matter inputs to soil food webs. Vegetation also provides fuel for fire, as well as resources and habitat structure for belowground and aboveground organisms ranging from fungi and bacteria to birds and large mammals (Whitford 2002, Wardle 2002). Finally, carbon storage and the mediation of earth-atmosphere energy / water balances are additional vegetation functions that are increasingly emphasized by researchers investigating global-change processes (Breshears and Allen 2002, Asner et al. 2003).

A large number of vegetation attributes affect the manner and extent to which these many functions are performed. Size, biomass, photosynthetic rate, relative and absolute growth rates, tissue chemistry, basal cover, canopy cover, canopy structure, spatial arrangement and contiguity, leaf area, leaf longevity, and life span are some of the more important vegetation attributes for ecosystem functioning (Chapin 1993). Root distribution, photosynthetic pathway, and phenology are additional functional attributes of vegetation that are particularly important in dryland ecosystems (Ehleringer et al. 2000, Whitford 2002). With respect to disturbance interactions, important functional attributes include palatability, flammability, and mode of post-disturbance regeneration.

Small trees, shrubs, dwarf shrubs, and perennial grasses are the vegetative life forms with the greatest effects on the structure and functioning of dryland ecosystems (Whitford 2002). In some dryland systems, annual grasses (typically exotic) also can have significant effects on ecosystem structure and function (e.g., Billings 1990, Belnap and Phillips 2001, Evans et al. 2001). The two most important tree genera in drylands of this region are *Juniperus* and *Pinus*. Important genera of shrubs and dwarf shrubs include members of the Asteraceae (*Artemisia*, *Chrysothamnus, Ericameria*, *Gutierrezia, Tetradymia,* and *Xylorhiza*), the Chenopodiaceae (*Atriplex*, *Grayia, Sarcobatus*, and *Krascheninnikovia*), the Rosaceae (*Cercocarpus, Purshia, Coleogyne,* and *Fallugia*), and the Ephedraceae (*Ephedra*). Important genera of perennial grasses include those characterized by the C_4 photosynthetic pathway (*Bouteloua, Muhlenbergia, Aristida, Pleuraphis*, and *Sporobolus*) and the C_3 photosynthetic pathway (*Acnatherum, Hesperostipa, Poa*, and *Festuca*). In general, the relative importance of C_3 versus C_4 perennial grasses in dryland ecosystems increases regionally with latitude and locally with elevation. Genera of annual grasses include *Bromus*, *Festuca*, and *Schismus*.

Many of the functional attributes described above differ greatly among vegetative life forms[5]. For example, there are relatively large differences among dryland trees, shrubs and perennial grasses in terms of canopy architecture and spatial arrangement, as well as in their responses to climate, fire and herbivory. As a consequence, ecosystems characterized by different proportions of trees, shrubs, and grasses can be

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[4] *Resistance* refers to the capacity of a particular ecosystem attribute or process to remain essentially unchanged from its reference state or dynamic despite exposure to a disturbance and/or stressor. *Resilience* refers to the capacity of a particular ecosystem attribute or process to recover to its former reference state or dynamic after exposure to a temporary disturbance and/or stressor (adapted from Grimm and Wissel 1997). *Resistance* and *resilience* are dynamic properties that vary in relation to environmental conditions (Scheffer et al. 2001).
[5] There also is significant functional variation *within* each of these life forms that must be considered with respect to the structure and functioning of specific ecosystems on a site-specific basis.

expected to differ greatly in terms of associated ecosystem processes including nutrient cycles, hydrologic cycles, disturbance regimes, and wildlife-habitat relationships. Likewise, temporal shifts in the relative abundance and spatial configuration of vegetative life forms can significantly affect the functioning of numerous ecosystem processes.

c. Soil Biota

Soil biota represent another broadly defined group of organisms that is a major contributor to the structure and functioning of dryland ecosystems. Most of the ecosystem processes described above in relation to soil resources (i.e., nutrient cycling, water infiltration and storage, soil aggregate stability) are mediated by soil organisms (Skujins 1984; Whitford 1996, 2002; Lavelle 1997; Wardle 2002). Although the general significance of soil biota for ecosystem processes (particularly nutrient cycling) has long been acknowledged, there is increasing recognition that this diverse group of organisms must be considered much more explicitly in order to develop a better understanding of the structure and functioning of terrestrial ecosystems (Bever et al. 1997, Wardle 2002, Reynolds et al. 2003). Because of their intimate association with other components of dryland ecosystems, soil biota in Figure 4 are included in components identified as soil resources, vegetation, biological soil crusts, and invertebrates.

Wardle (2002) noted that most terrestrial species occur in soil, and that the tremendous (and poorly understood) diversity of this group has added to the logistical difficulties posed by studying belowground organisms and processes. Soil biota include microfloral components (bacteria, algae, and fungi), microfaunal components (nematodes, microarthropods, and protozoans), and macrofaunal components (earthworms, ants, termites, and larval stages of several insect families) that are involved in a variety of processes essential for litter decomposition and nutrient cycling. Functioning of these belowground processes is dependent on the amounts and types of organic-matter inputs from vegetation and on soil conditions such as moisture availability, soil structure, soil aeration, and soil temperature (Whitford 1996, 2002; Wardle 2002).

Soil biota also include mycorrhizal fungi that form symbiotic associations with roots of many plant species. The mycorrhizal symbiosis is one in which the fungal partner provides nutritional benefits to the host plant, and the plant provides carbohydrates to the fungi (Smith and Read 1997). Roots colonized by mycorrhizal fungi acquire phosphorus, zinc, and possibly copper and N more efficiently than uncolonized roots. There is also evidence that mycorrhizae can increase water uptake in plants due to the greater soil volume accessed by colonized roots (Smith and Read 1997). Due to their role in enhancing resource availability to colonized plants, mycorrhizae have been found to mediate competitive relations between plants with differing responses to mycorrhizal colonization (Allen and Allen 1990, Marler et al. 1999). Recent work also has shown that the diversity of mycorrhizal fungi can determine the diversity and productivity of vascular plant communities (van der Heijden et al. 1998).

Some species in most of the plant families common to dryland ecosystems have been identified as mycorrhizal when inspected by botanists (Trappe 1981). Families with a high frequency of mycorrhizal colonization among inspected species include the Asteraceae, Fabaceae, Rosaceae, Poaceae, and Solanaceae. Frequency of colonization among inspected species in the Chenopodiaceae and Cactaceae is much lower, although mycorrhizal species have been found. The Brassicaceae stands out as a common dryland plant family in which most inspected species are nonmycorrhizal (Trappe 1981).

Another important symbiotic relationship involving soil biota is that between plants and N-fixing bacteria. Several shrubs that are locally common or abundant throughout the Colorado Plateau region are capable of forming a symbiotic association with N-fixing actinomycetes in the genus *Frankia*. Actinorhizal shrub genera of the region include *Cercocarpus* and *Purshia* (Rosaceae), *Shepherdia* (Elaeagnaceae), and *Ceanothus* (Rhamnaceae) (Baker and Schwencke 2000, cited by Schwencke and Carú 2001). The frequency of actual actinorhizal colonization in these genera and the overall contributions of this relationship to dryland N cycling are poorly understood. However, it is significant that all of the actinorhizal shrub genera in the region are important forage resources both for wild herbivores and for domestic livestock, suggesting that the actinorhizal relationship may be a factor affecting forage preferences.

d. Biological Soil Crusts

Biological soil crusts (BSC's) are biotic communities composed of cyanobacteria, algae, microfungi, mosses, and lichens that occur on and within the upper few millimeters of the soil surface (Belnap et al. 2001). These diverse communities are characteristic biotic components of ecosystems where environmental conditions limit the development of closed-canopy vascular plant communities or thick layers of surface litter (Belnap et al. 2001a). They are particularly prominent features in drylands of the Colorado Plateau region where much pioneering work has been conducted concerning their environmental relationships, disturbance responses, and ecological functions (e.g., Rosentreter and Belnap 2001, Belnap 2002, Bowker et al. 2002).

In addition to their major contributions to biological diversity, BSC's perform several functions in dryland ecosystems. The presence and physiological activity of BSC organisms aggregate soil particles, thereby increasing soil stability and reducing the susceptibility of soil to erosion by wind and water (Williams et al. 1995a,b). Surface characteristics and stability of BSC's also favor the capture and retention of aeolian sediments that can be significant sources of mineral nutrients in dryland ecosystems (Belnap et al. 2001b, Reynolds et al. 2001). BSC's similarly can capture and enhance ecosystem retention of windborne and waterborne organic matter and seeds (Belnap et al. 2001b).

Hydrologic effects of BSC's are complex, with few generalizations possible due to variations in relation both to soil factors and BSC factors. [The following synthesis is largely drawn from the recent review by Warren (2001).] Above-ground structures of BSC's intercept rainfall, thereby reducing raindrop impact and erosivity, and reducing the detachment of soil particles that can clog soil pores and inhibit infiltration. In this function, cyanobacteria and algae are less effective than mosses and lichens. Based on available evidence, BSC's on sandy soils (> 80 percent sand content) with inherently high infiltration capacities tend to reduce infiltration relative to soils of similar texture without BSC's because BSC organisms block pore spaces near the soil surface. However, adverse effects of BSC's on infiltration in sandy soils may be mitigated by effects of BSC's on soil-surface roughness. In cool-desert regions such as the Colorado Plateau, frost heaving can result in BSC's with pinnacled or rolling soil-surface microtopography (Belnap 2001a). Where these microtopographic features significantly enhance soil-surface roughness, the velocity of overland flow may be reduced, thereby increasing the residence time of runoff on hillslopes, enhancing slope retention of water and waterborne sediment, and facilitating water infiltration. This soil-roughness hypothesis has not been tested experimentally.

On relatively fine-textured soils, BSC effects on hydrologic processes can differ from those found on sandy soils – although the soil-roughness hypothesis still applies (Warren 2001). Compared with sandy soils, soils with a significant percentage of clay-sized particles are characterized by lower porosity and lower inherent infiltration capacities. Organic carbon produced by BSC organisms can contribute to the formation of stable soil aggregates that increase the ratio of macro- to micropores and thus enhance infiltration. Due to enhanced soil aggregate stability, fine-textured soils with BSC's are likely to have higher infiltration rates than soils of similar texture without BSC's. However, in silty soils where a *vesicular horizon*[6] subtends the BSC layer and controls soil infiltration capacity, the presence of BSC organisms is unlikely to enhance infiltration except through the hypothesized soil-roughness effect (e.g., Dobrowolski 1994).

In addition to enhancing soil stability and the retention of nutrients in sediment and organic matter, BSC's contribute to dryland nutrient cycles in other ways. Mosses, cyanobacteria, green algae and lichens all are photosynthetic and thus are significant sources of carbon in dryland ecosystems, particularly in interspaces among vascular plants where soil crusts can attain 100 percent cover (Lange 2001). Cyanobacteria (e.g., *Microcoleus*, *Nostoc*, and *Scytonema*) and cyanolichens (e.g., *Collema* and *Peltigera*) also are capable of fixing atmospheric N into a mineral form that can be used by vascular plants (Evans and Lange 2001, Belnap 2002). Although actinorhizal shrubs also are likely contributors to N cycles in the region (see above), the ubiquity of BSC's relative to actinorhizal shrubs suggests that the former are the major N contributors in the region (Evans and Ehleringer 1993, Belnap 2002). Soil crust organisms are significant food sources for other soil biota, particularly enhancing the activity of soil food webs in interspaces among vascular plants

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[6] Vesicular A horizons up to several mm thick are common at the surface of silty desert soils. Vesicular structure is characterized by a large volume of spherical soil voids that appear to form when soil air is entrapped in wetted soil. Presence of a vesicular horizon greatly reduces soil hydraulic conductivity (Hillel 1998, Birkeland 1999).

(Belnap 2001b). BSC's also affect the nutrient cycling activities of soil food webs through their effects on near-surface moisture availability, soil structure, soil aeration, and soil temperature (Belnap 2001b).

BSC's influence vascular plants in a variety of ways. Effects of BSC's on soil-surface stability and roughness result in seed-bed characteristics that differ greatly from those of soils without BSC's. As with sediment and other organic materials, seed catchment and retention are generally enhanced by the presence of BSC's. Belnap and colleagues (2001b) reviewed the literature concerning effects of BSC's on plant establishment and found that research results varied depending on BSC characteristics: plant species investigated, methods of study, and environmental conditions. BSC's are best viewed as environmental sieves that favor or discourage plant establishment, depending on environmental conditions and on species-specific attributes such as propagule morphology and germination requirements. If a generalization is possible, it is that BSC's tend to inhibit establishment of annuals and species without specialized burial mechanisms such as twisting awns (Belnap et al. 2001b). In southeastern Utah, Howell (1998) found that BSC's inhibited establishment of the exotic grass *Bromus tectorum*. Following the establishment phase, plants growing in soils with BSC's generally have been found to have greater biomass and lower root:shoot ratios than comparable plants growing in soils without BSC's, suggesting greater availability of soil resources in the presence of BSC's (Belnap et al. 2001b). Relative to plants growing in soils without BSC's, plants growing in association with N-fixing cyanobacteria and cyanolichens consistently have greater N concentrations in tissues and usually have higher concentrations of plant-essential nutrients potassium, magnesium, copper, and zinc (Harper and Belnap 2001). In contrast, plants growing in soils with BSC's commonly have lower concentrations of phosphorus and iron than plants growing in soils without BSC's, suggesting that plants and BSC's may compete for these elements. Nutritional differences between plants grown in soils with and without BSC's are greatest in shallow-rooted herbaceous species, probably because they are rooted in near-surface soils that are most directly influenced by BSC's (Harper and Belnap 2001).

e. Invertebrate and Vertebrate Consumers

Vertebrate and invertebrate consumers are significant contributors to the biological diversity of dryland ecosystems in the region (e.g., Nelson 1994, Griswold et al. 1997, Hanna and Graham 2003, San Miguel and Colyer 2003). There are numerous ways in which above-ground consumers can directly or indirectly affect the structure and functioning of dryland ecosystems (Whitford 2002). Activities associated with granivory and herbivory are among those that have the greatest ecosystem-level consequences due to their many effects on vegetation structure and soil processes. Processes of competition and predation likewise can have important ecosystem-level consequences by altering the structure of consumer food webs, but these processes are not reviewed here.

Granivory is one of the most-studied processes in dryland ecosystems, although most research on this topic has been conducted outside the region encompassed by this report. Organisms that can be important granivores in dryland ecosystems of the region include harvester ants, beetles, rodents and frugivorous mammals, and birds (Chambers et al. 1999, Whitford 2002). Through selective harvesting, consumption, and dispersal via caching and defecation, granivores can have strong effects on the abundance, composition, and spatial distribution of the seed bank (Whitford 2002). Through time, these seed-bank effects can be reflected in the composition and spatial structure of plant communities. For example, seed hoarding and caching behaviours of corvids such as Steller's jays (*Cyanocitta stelleri*) and Clark's nutcrackers (*Nucifraga columbiana*) have been implicated in the up-slope migration of piñon in the Southwest (Chambers et al. 1999). In desert grasslands of southeastern Arizona, Brown and Heske (1990) proposed that selective seed harvesting and soil disturbance by kangaroo rats (*Dipodomys* sp.) were responsible for major changes observed in vegetation structure over a 12-year period. However, on the basis of subsequent studies, Whitford (2002) questioned whether the hypothesized mechanisms were sufficient to explain the observed vegetation changes. Whitford (2002) also suggested that effects of granivorous rodents and ants on soils (i.e., resource enrichment through excretion and soil disturbance through burrowing) could have greater impacts on dryland vegetation structure than granivory itself.

Like granivory, herbivory can have numerous direct and indirect effects on ecosystem properties. Native herbivores in dryland ecosystems of the region include insects (grasshoppers, bark beetles, and many others), and mammals such as woodrats (*Neotoma* spp.), desert cottontails (*Sylvilagus audubonii*), black-tailed jackrabbits (*Lepus californicus*), bighorn sheep (*Ovis canadensis*), pronghorn (*Antilocapra americana*), and mule deer (*Odocoileus hemionus*). In some locations, elk (*Cervus elaphus*) use of dryland systems also

can be significant, particularly in winter (Allen 1989). Herbivorous insects and small to medium-sized mammals can have significant effects on vegetation structure and ecosystem processes such as nutrient cycling. With the exception of infrequent insect outbreaks (discussed below as a disturbance), the greatest ecosystem-level consequences of herbivory are those that can be caused by high densities of large-bodied browsers and grazers such as mule deer, elk and domestic livestock.

Large herbivores can affect individual plants both directly and indirectly through a variety of mechanisms. Direct impacts include altered physiological function and morphology attributable to defoliation and trampling (Briske 1991, Briske and Richards 1995). Defoliation and trampling by large herbivores may indirectly influence plant performance as a consequence of altered microenvironmental conditions, soil properties (Thurow 1991), mycorrhizal relations (Bethlenfalvay and Dakessian 1984), competitive relations, and through effects on ecosystem processes such as nutrient cycling and hydrology. Seed dispersal is yet another indirect mechanism by which large herbivores and other animals may affect vegetation structure. Through time, combined direct and indirect impacts can result in altered plant population dynamics (e.g., altered rates of reproduction, recruitment, and mortality) and consequent changes in plant community composition, structure, and distribution (Crawley 1983, Archer and Smeins 1991, Archer 1994, Miller et al. 1994, Bich et al. 1995). Due to strong interactions of vegetation with nutrient cycling, hydrologic processes, disturbance regimes, and geomorphic processes, herbivore-driven changes in vegetation structure can have cascading effects on multiple ecosystem processes and properties.

Considerable debate has occurred concerning the consequences of herbivory for plant productivity (e.g., McNaughton 1983, 1986, 1993; Belsky 1986, 1987; Painter and Belsky 1993; Dyer et al. 1993). This debate has centered on the phenomenon of "compensatory growth" in defoliated plants. Compensatory growth is generally defined as a positive response of plants to injury by defoliation (Belsky 1986). McNaughton (1983:329) described the phenomenon as follows:

> "Compensatory growth in plants subjected to herbivory may alleviate the potential deleterious effects of tissue damage, whether to vegetative or reproductive organs. Tissue destruction is rarely, if ever, translated monotonically into a proportional reduction of final yield. Internal mechanisms of compensation involve modifications of plant metabolism; external mechanisms of compensation involve modifications of the plant environment that are favorable to plant growth and yield."

Belsky (1986) clarified the discussion by subdividing the term "compensation" into three separate terms (Table 2).

Table 2. Compensatory growth of plants in response to tissue removal (modified from Belsky 1986).

Possible Plant Responses to Defoliation	Productivity of Defoliated (D) Plant in Relation to that of Undefoliated (U) Plant	Growth Compensation (%)
1. Overcompensation	D > U	>100
2. Exact compensation	D = U	100
3. Undercompensation	D < U	<100
a. Partial compensation	D < U	1-99
b. No compensation	D < U	0
c. Damage	D < U	<0

Numerous physiological (internal) and/or microenvironmental (external) mechanisms may contribute to the occurrence of compensatory growth in plants (Crawley 1997). For example, remaining foliage may experience increased relative growth rates due to diminished shading and increased light levels following grazing (a microenvironmental mechanism), or remaining foliage of a grazed plant may experience greater above-ground growth due to the reallocation of resources from root growth (a physiological mechanism). In general, the potential for and significance of compensatory growth is believed to vary in relation to the timing of herbivory, the frequency and intensity of herbivory, the availability of resources both within the plant and in the surrounding soil environment (water and mineral nutrients), as well as the presence and competitive ability of neighboring plants (Briske and Richards 1994, 1995; Crawley 1997). Given the importance of resource availability for the occurrence and significance of compensatory growth, DeAngelis and Huston

(1993) and Bartolome (1993) reasoned that overcompensation was most likely to occur in productive, intensively managed systems rather than in resource-poor environments characteristic of dryland ecosystems. In a review concerning the physiological responses of plants to grazing, Briske and Richards (1994:169) concluded that (1) compensatory mechanisms only infrequently increase the total growth of defoliated plants above that of undefoliated plants (i.e., "overcompensation" is rare), and (2) application of the concept to management of wildland vegetation is unwarranted because the phenomenon is so complex and poorly understood.

Although compensatory growth of individual plants may occur, alteration of competitive relations among defoliated or differentially defoliated plants is of greater consequence for plant populations and communities (Briske 1991, Archer and Smeins 1991, Briske and Richards 1994, Crawley 1997). Plants that are defoliated less frequently or less intensively experience a competitive advantage relative to plants that are defoliated more frequently or more intensively. Similarly, plants that possess a greater capacity for regrowth following defoliation experience a competitive advantage over plants that possess a lesser capacity for regrowth. Thus for an individual plant, the most significant benefit arising from herbivory is diminished competition from a neighboring plant that has been reduced in size and competitive ability by an herbivore (e.g., Caldwell et al. 1987). Plants that benefit most from herbivory are those species which are least palatable or accessible to herbivores and therefore most likely to derive competitive benefits from the defoliation of neighboring plants. Through time, altered competitive relations eventually can be expressed in population dynamics and plant community structure (Briske 1991).

Large herbivores also can affect the productivity and composition of plant communities through numerous indirect and direct effects on nutrient cycling (Archer and Smeins 1991). Herbivore-driven shifts in plant community structure can affect nutrient cycles by altering the capacity of vegetation to capture and retain soil and water resources (Whitford 2002) and by altering the quantity and quality of organic-matter inputs (Bardgett and Wardle 2003, Reeder et al. 2004). Herbivory removes foliage and directly diverts nutrients from litter and physiological processes of intra-plant cycling. Nutrients acquired from foliage may be incorporated in animal biomass or spatially redistributed across the landscape in urine and dung. Where excreta are deposited, productivity may be enhanced if nutrients contained in the excreta are accessible to nearby plants. In other portions of the landscape, productivity may be reduced due to the removal of nutrients in foliage.

Significant losses of nutrients from ecosystems may occur as a consequence of herbivory (Archer and Smeins 1991, West 1991). A significant proportion of the N consumed in foliage is lost to the atmosphere in gaseous products of digestion and through volatilization of ammonia from dung and urine. In ecosystems where dung beetles are not present to bury feces and cycle nutrients through soil food webs (including much of the Colorado Plateau region), up to 80 percent of fecal N may be lost to volatilization, with greatest losses expected from sandy, high-pH soils (Woodmansee 1979). Schimel et al. (1986) found lower rates of N loss from cattle urine, possibly because urine enters the soil more readily than dung. These researchers reported higher N losses from cattle urine in coarse soils (12-27 percent) than from fine-textured soils (0-2 percent).

In dryland ecosystems where components of biological soil crusts are the predominant sources of N inputs, trampling by large herbivores also can have direct effects on nutrient cycling. Evans and Ehleringer (1993) found that N-fixing cyanobacteria and cyanolichens in biological soil crusts were the primary sources of N inputs to a piñon-juniper ecosystem in southern Utah. They hypothesized that trampling disturbance of biological soil crusts could eventually result in long-term ecosystem degradation due to diminished N inputs by damaged or eliminated N-fixing crust organisms. In southeastern Utah, Evans and Belnap (1999) compared soil N dynamics between an ungrazed grassland and an adjacent grassland that experienced intermittent winter grazing by livestock prior to 30 years ago. Cover of N-fixing cyanolichens was 5.5 percent in the ungrazed grassland and less than 1 percent in the formerly grazed grassland. Compared with the formerly grazed grassland, the ungrazed grassland was characterized by soil-crust N fixation rates that were 250 percent greater and soil N content that was 135-250 percent greater. The authors concluded that soil disturbance had resulted in long-term consequences for N cycling and storage in the dryland ecosystem they studied. Thus although some plants may benefit from localized resource enrichment attributable to herbivore excreta, the literature suggests that the long-term consequence of herbivory and trampling by large ungulates in dryland ecosystems could be a gradual ecosystem-level decline in N fertility. Following a review of mechanisms by which aboveground and belowground herbivores affect nutrient cycling, Bardgett and

Wardle (2003) concluded that positive effects of herbivory on soil processes and soil biota are most common in ecosystems with high soil fertility and relatively high consumption rates, whereas adverse effects are most common in low-fertility ecosystems with relatively low consumption rates.

In addition to impacts of trampling on N inputs where biological soil crusts are present, repeated trampling by large herbivores can destabilize soils and result in the depletion of rock-derived nutrients through the aeolian loss of fine soil particles. For example, Neff and colleagues (*in press*) found lower content of fine soil particles and rock-derived nutrients at a formerly grazed site relative to an ungrazed site at the Needles District of Canyonlands National Park. On the basis of soil magnetic properties which indicate the presence of far-travelled aeolian dust in these sandstone-derived soils, the authors attributed soil differences between the two sites to accelerated wind erosion caused by destabilizing effects of repeated trampling at the grazed site. Because of the strong positive relationship between soil magnetic susceptibility and several lab-based measures pertaining to the bioavailability of rock-derived nutrients in sandstone-derived soils (e.g., cation exchange capacity, silt content, phosphorus and potassium bioavailability), magnetic susceptibility shows promise as an indicator of long-term soil-surface stability in some Colorado Plateau landscapes (e.g., Fig.7).

Some workers have hypothesized that trampling by large herbivores has beneficial impacts on infiltration (Savory and Parsons 1980, Savory 1988). However, an extensive amount of hydrologic research has failed to support this hypothesis (Spaeth et al. 1996, Holechek et al. 2000), indicating instead that trampling tends to result in lower infiltration rates where it destroys stable soil aggregates and leads to a deterioration of soil structure (Thurow 1991). Hydrologic impacts of trampling by large herbivores vary in relation to soil type (e.g., texture and the presence of a vesicular A horizon), soil water content, seasonal climatic conditions, vegetation type, and the magnitude of trampling (Thurow 1991).
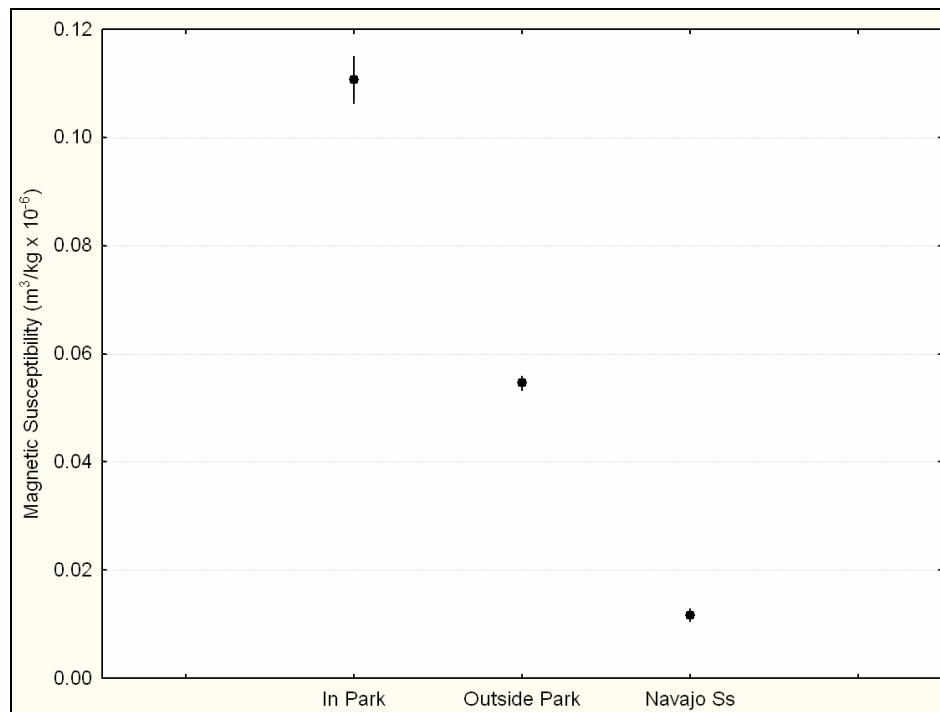
Figure 7. Magnetic susceptibility (mean ± 1 SE) of surficial sediments at a formerly grazed grassland site in the Island in the Sky District of Canyonlands National Park (ungrazed for 30 years), a currently grazed grassland site outside the Park, and of Navajo Sandstone bedrock – the principle parent material for soils at both sites. Soils at both sites are classified as Begay fine sandy loams (coarse-loamy, mixed, mesic Ustollic Camborthid).

4. Natural Disturbance Regimes

a. Background

A *disturbance* is "...any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett 1985:7). For purposes of ecosystem management and monitoring, disturbances are considered to be ecological factors that are within the range of conditions naturally experienced by the ecosystem (e.g., drought). These are differentiated from *stressors*, which may fit the definition of disturbance but are outside the range of disturbances naturally experienced by the ecosystem and typically are anthropogenic in origin (Whitford 2002). Implicit in the "natural" aspect of these definitions is the need to identify ecosystem-specific reference conditions which are framed with respect to a particular time period and place (White and Walker 1997, Landres et al. 1999). In addition to these temporal and spatial bounds, ecosystem managers should explicitly identify associated goals, assumptions, and value judgements when adopting a particular set of reference conditions as the "natural" standard for management and monitoring (Truett 1996, Landres et al. 1999). Late-Holocene, pre-European conditions often are identified as the standard for defining natural disturbance regimes, although it is important to recognize the potentially important role of pre-European human populations in shaping disturbance regimes and ecosystem conditions found at the time of European contact (Betancourt and Van Devender 1981, White et al. 1999).

In addition to climatic fluctuations, disturbances are major drivers of ecosystem change and variability. Disturbance is a factor affecting the spatial and temporal dynamics of all ecosystems, but disturbances differ greatly among ecosystems in relation to climate, topography, substrate, and ecosystem attributes such as vegetation structure. Disturbances can be differentiated on the basis of several descriptors which, taken in combination, characterize the *disturbance regime*. Descriptors of disturbance regimes include the kind of disturbance (e.g., surface fire versus windthrow), spatial characteristics (e.g., patch size, spatial extent and patterning), temporal characteristics (e.g., frequency, timing, return interval), specificity (e.g., selective effects by species, age class, or landscape unit), magnitude (e.g., intensity, severity), and synergisms (e.g., interactions with other disturbances) (Sousa 1984, White and Pickett 1985, White et al. 1999). Most ecosystems experience more than one type of disturbance, and interactions among disturbances commonly occur because particular disturbance events can affect the capacity of ecosystem components or processes to resist or recover from subsequent disturbances. Similarly, interactions can occur between natural disturbances and anthropogenic stressors (White et al. 1999, Archer and Stokes 2000). Because disturbances play such an important role in shaping the structure and functioning of ecosystems (strongly interacting with soil resources and vegetation structure), disturbance-regime alteration is one of the most common ways by which human activities affect the functioning and sustainability of ecosystems (Chapin et al. 1996).

b. Extreme Climatic Events

Episodic climatic events are major disturbances in dryland ecosystems (Walker 1993, Whitford 2002). Drought, extreme precipitation events and floods, and wind storms can induce long-term changes in ecosystem structure and function by causing widespread mortality or enabling establishment of long-lived plants that are structural dominants. The erosive energy of extreme precipitation and wind events also can result in massive transport and redistribution of soil resources, potentially inducing geomorphic changes that fundamentally alter site conditions. Event sequencing (e.g., timing of flood in relation to drought) is an important factor that can affect ecosystem resistance and resilience to episodic climatic events. Although episodic, event-driven change is an important feature of many ecosystems (Holling 1996, Scheffer et al. 2001), it is particularly characteristic of dryland ecosystems (Whitford 2002). Examples from this region include the 1950's drought that affected the structure of piñon-juniper woodlands throughout much of the Southwest (Betancourt et al. 1993, Allen and Breshears 1998), as well as the recent severe drought (the "early 21st century drought" of Webb et al. 2004) that has caused region-wide mortality in piñon and sagebrush (*Artemisia* sp.). Climatic conditions and events can affect ecosystem susceptibility to other disturbances such as fire and insect outbreaks (Swetnam and Betancourt 1998), as well as affect ecosystem resistance and resilience to anthropogenic stressors (Archer and Stokes 2000, Scheffer et al. 2001).

c. Fire

Fire is another type of natural disturbance that can have many direct and indirect effects on the structure and functioning of dryland ecosystems. One of the most significant effects of fire is the alteration of vegetation composition and structure due to the selective damaging or elimination of fire-intolerant life forms or age classes (Whelan 1995). Specific effects of fire on vegetation structure vary in relation to fire-regime characteristics (e.g., frequency, intensity, seasonality, and spatial patterning) and fire responses of dominant vegetative life forms. Fire-regime characteristics are strongly influenced by the vegetation itself, as well as by preceding and coincident weather conditions that affect fuel availability, fuel flammability, and fire behaviour. In some dryland ecosystems, low-intensity surface fires play a role in thinning or eliminating fire-intolerant woody vegetation and favoring the relative dominance of relatively fire-tolerant graminoids (Jameson 1962, Wright 1980). In systems where repeated surface fires are required to maintain grassland- or savanna-like physiognomic structure, the necessary fire frequency depends on the amount of time needed for predominant woody taxa to (1) develop features that confer resistance to surface fires (e.g., thick bark and elevated canopies) or (2) competitively exclude herbaceous taxa that provide fine fuels to support surface fires.

Effects of fire on vegetation structure have multiple ecosystem-level consequences due to strong vegetation interactions with soil, hydrology, and geomorphic processes. Fire-caused reductions in vegetative cover can result in significant runoff and erosional losses of soils, nutrients and organic matter by water and wind. However, long-term effects of fire on vegetation structure (e.g., promotion of greater graminoid cover) may cause a net decrease in runoff and erosion. Most fire effects on wildlife also are mediated through effects on vegetation structure and nutritional quality of forage.

Fire also has significant ecosystem-level consequences due to effects on nutrient cycles (Raison 1979; Blank et al. 1994a,b). Depending on the type and intensity of fire events, fire can (1) increase nutrient *bioavailability* on a short-term basis due to ash deposition and accelerated rates of nutrient cycling, and (2) deplete total nutrient *stocks* due to gaseous losses (particularly N) and off-site transfers of ash (Raison 1979). Nutrients losses in gases and ash are generally proportional to heat generated and organic-matter consumed by fire (Raison 1979, Schlesinger 1997). Depending on fire severity, other soil characteristics can be affected by fire, including pH (typically increased by ash deposition), cation exchange capacity and infiltration capacity (both typically decreased by organic-matter losses and transformations) (Raison 1979).

Natural fire regimes vary greatly among dryland ecosystems of the Colorado Plateau region. Fire generally is insignificant as a natural disturbance in sparse desert shrublands dominated by taxa such as *Atriplex confertifolia*, *A. corrugata*, *Coleogyne ramosissima*, and *Sarcobatus vermiculatus*; as well as in semidesert grasslands dominated by taxa such as *Acnatherum hymenoides*, *Hesperostipa comata*, *Aristida* spp., *Sporobolus* spp., and *Pleuraphis jamesii*. These grasslands have been described as "galleta – three-awn shrub steppe" (Küchler 1964, West and Young 2000) and are characteristic of CANY, CARE, ARCH, GLCA, and CHCU.

In contrast with these fuel-limited systems where fire is of minimal importance, fire is a significant natural disturbance in several other dryland ecosystems of the region. These include sagebrush shrublands and shrub steppe (e.g., DINO, FOBU, BLCA), relatively productive semidesert grasslands and juniper savannas (e.g., WUPA; Jameson 1962, Johnsen 1962), and piñon-juniper woodlands and forests (e.g., MEVE, ZION). Miller and colleagues (1994) estimated that natural fire-return intervals in sagebrush steppe varied from 20-30 years in mountain big sagebrush systems (*Artemisia tridentata* var. *vaseyana*) to 50-100 years in Wyoming big sagebrush systems (*A. tridentata* var. *wyomingensis*) prior to the introduction of livestock and effective fire suppression. However, caution is warranted regarding generalizing from these estimates since they were derived from observations made in Great Basin ecosystems rather than Colorado Plateau ecosystems. Fire-history studies in sagebrush systems are hampered by the absence of plant species that record fires by means of datable scars.

Natural fire regimes in ecosystems vegetated by various species of piñon and juniper are poorly understood. Contributing factors include the tremendous structural and functional diversity of systems broadly categorized as piñon-juniper vegetation types (e.g., Harper et al. 2003), and the relative lack of area-specific fire-regime studies conducted in such systems across the region (Baker and Shinneman 2004). In a systematic review of the natural role of fire in piñon-juniper ecosystems, Baker and Shinneman (2004)

concluded that (1) spreading, low-severity surface fires probably were uncommon in such ecosystems prior to EuroAmerican settlement, and (2) much additional area-specific research is urgently needed to provide a foundation for science-based management and restoration efforts. In this latter conclusion, they are in agreement with other workers who have warned ecosystem managers not to rely uncritically on fire-regime generalizations derived from studies conducted elsewhere (e.g., Veblen 2003, Romme et al. 2003a).

Some of the most extensive work on piñon-juniper fire regimes on the Colorado Plateau has been conducted at MEVE. Floyd and colleagues recently estimated that the natural fire rotation time (amount of time required to burn an area equal in size to the entire area under consideration) in piñon-juniper ecosystems at MEVE is approximately 400 years (Floyd et al. 2000, 2003b, 2004; Romme et al. 2003a). No fire scars indicative of surface-fire occurrence have been located at MEVE despite extensive searching. Instead, minimum stand ages ranging from 200 to over 400 years indicate that the natural piñon-juniper fire regime at MEVE is one characterized by infrequent, stand-replacing canopy fires. In a study conducted on the Uncompahgre Plateau north of MEVE, Eisenhart (2004) also concluded that (1) there was no evidence to support the idea that frequent, low-severity surface fires were common in any piñon-juniper ecosystems in her study area, and (2) the predominant natural disturbance regime in these ecosystems is infrequent, stand-replacing canopy fire.

In an attempt to clarify issues associated with piñon-juniper fire regimes, Romme and colleagues (2003a) proposed a framework describing a set of hypotheses concerning variations in piñon-juniper structure, function, and status (Table 3). They identified three types of piñon-juniper systems that are fundamentally different in these respects. Of the three types, the authors hypothesized that only the *piñon-juniper grass savanna* is characterized by a natural fire regime consisting of frequent, low-severity surface fires (Table 3). Grasslands and juniper savannas found in and around WUPA exemplify this type of system (Jameson 1962, Johnsen 1962), as did significant proportions of the landscape at BAND prior to the introduction of livestock in the 19th century (Allen 1989). The *piñon-juniper shrub woodland* is a vegetation type with a natural disturbance regime that involves moderately frequent stand-replacing fire carried by shrub and tree canopies (Table 3, Romme et al. 2003a). The authors hypothesize that the natural post-fire successional sequence in this type proceeds from herb dominance, to shrub dominance, to a mixed shrub-tree community (with young trees) before the sequence is reset by a stand-replacing fire. Evidence exists to suggest that this type of dynamic may be naturally characteristic of some sagebrush ecosystems on the Colorado Plateau (e.g., Rowlands and Brian 2001, Harris et al. 2003). Finally, the studies conducted at MEVE (Floyd et al. 2004) and on the Uncompahgre Plateau (Eisenhart 2004) provide evidence for the third type of system – *piñon-juniper forests* – which is characterized by infrequent, stand-replacing fires carried by tree canopies.

d. Insect and Disease Outbreaks

Although insect and disease outbreaks can be important natural disturbances, the roles of such phenomena in dryland ecosystems are poorly understood relative to montane and boreal forests where insects are recognized as major agents of disturbance (e.g., Veblen et al. 1991, Logan et al. 2003). It is believed that the occurrence of insect outbreaks in tree-dominated ecosystems is linked with climatic conditions that diminish the vigor and insect resistance of host plants and/or affect life cycles and dispersal patterns of insect herbivores (Swetnam and Betancourt 1998, Logan et al. 2003). In piñon-juniper ecosystems, outbreaks of the bark beetle *Ips confusus* (piñon ips) can be triggered by drought conditions that weaken host-tree populations (Leatherman and Kondratieff 2003). Drought and ips beetle outbreaks in combination can act as broad-scale disturbances in these systems, as reflected by the massive mortality that has occurred recently in piñon populations across the southern Colorado Plateau region in response to the early 21st century drought. As with fire, insect outbreaks thus can interact with climate to generate long-term changes in vegetation structure. Insect- or pathogen-generated changes in vegetation structure can have multiple ecosystem-level consequences due to vegetation interactions with nutrient cycles, hydrologic processes, and geomorphic processes.

Table 3. Structure, disturbance dynamics, distribution patterns, current status, and restoration needs of three contrasting types of piñon-juniper ecosystems in western North America: A synthesis and set of hypotheses for further research. HRV = historic range of variability (from Romme et al. 2003a:346).

	Piñon-Juniper Grass Savanna	Piñon-Juniper Shrub Woodland	Piñon-Juniper Forest
Pre-1900 fire regime	frequent, low-severity, surface fires...caried by grasses	moderately frequent, high-severity, crown fires...carried by shrubs & trees	very infrequent, very high-severity, crown fires...carried by tree crowns
Pre-1900 stand structure	sparse trees, few shrubs, dense grass and other herbs	sparse to moderately dense trees, sparse to very dense shrubs, moderately denst to sparse herbs...all depending on time since last fire	dense trees, sparse to moderately dense shrubs, sparse herbs
Pre-1900 stand dynamics	low tree density and high herbaceous biomass maintained in part by recurrent fire	seral trend from herb to shrub to tree dominance, interrupted periodically by fire which returns a stand to early seral herb dominance	stable/stationary tree age structure and little change in shrub or herbaceous layers during the long intervals without fire...very slow recovery after fire
Post-1900 changes in disturbance regime	reduced fire frequency, great increase in fire severity	reduced fire frequency, small increase in fire severity	little change in fire frequency or fire severity
Post-1900 changes in structure	increasing tree density, decreasing herbaceous biomass	increasing tree density, decreasing shrubs and herbs	little change in tree density or in shrubs or herbs
Overall current status	outside HRV for disturbance regime, structure, & composition	outside HRV for disturbance regime, structure, & composition	still within HRV for disturbance regime, structure, & composition
Implications for restoration	urgent need for active restoration	urgent need for active restoration	no need for restoration...protect instead
Current stand age structure	very old trees (> 300 years) present, but not numerous...young trees (< 150 years) dominate stands	very old trees (> 300 years) absent or rare...young trees (< 150 years) dominate stands	very old trees (> 300 years) numerous...stands with all-aged structure, including old & young trees
Distribution: soil characteristics	deep, fine-textured soils	deep, fine-textured soils	shallow, rocky, or coarse-textured soils
Distribution: precipitation regime	summer peak in precipitation	winter peak in precipitation	variable
Distribution: topographic characteristics	gentle plains and broad valley bottoms, with few barriers to fire spread	gentle plains and broad valley bottoms, with few barriers to fire spread	rugged slopes, canyons, and mesa tops, with many barriers to fire spread
Distribution: adjacent vegetation types	grasslands, ponderosa pine, or other types that burn frequently	grasslands, big sagebrush, or other types that burn frequently	desert scrub, "slickrock," or other types with sparse herbaceous vegetation that rarely burn
Geographic distribution	most common in northern Mexico, southern New Mexico & Arizona, northern New Mexico, and possibly southeastern Colorado	most common in the northern and central Great Basin, and the Colorado Plateau	scattered throughout the Colorado Plateau, Great Basin, central Oregon, southern Rocky Mountains, and southern California mountains
Examples	Jameson 1962, Dwyer and Pieper 1967, Allen 1989, Segura and Snook 1992, Dick-Peddie 1993, Miller 1999	Tausch et al. 1981, Koniak 1985, Tausch and West 1988, Miller et al. 1995, Miller and Tausch 2001	Tausch et al. 1981, Tress and Klopatek 1987, Kruse and Perry 1995, Wangler and Minnich 1996, Miller et al. 1999, Tausch and Nowak 1999, Floyd et al. 2000, Waichler et al. 2001, Floyd et al. 2004

e. Herbivory and Trampling

Herbivory and trampling are additional natural disturbances in dryland ecosystems of the region. Potential ecosystem-level effects of herbivory and trampling were discussed above, but actual effects will vary in relation to ecosystem characteristics (e.g., climatic conditions, soil properties, and vegetation structure and composition) and disturbance characteristics. As with other disturbances such as fire, a key consideration for ecosystem management and monitoring is the *regime* of herbivory and trampling that is considered natural for particular ecosystems.

Predominant types of herbivores and the spatial patterning, temporal patterning, magnitude, selectivity, and synergistic relationships of herbivory and trampling likely varied among dryland ecosystems prior to

European settlement. At the time of contact, large native ungulates such as elk and bison (*Bison bison*) were uncommon in most dryland ecosystems of the Intermountain West in comparison with the Great Plains region east of the Rocky Mountains (Mack and Thompson 1982, Grayson 1994). Probable factors affecting regional-scale variations include landscape characteristics (e.g., availability of forage and perennial water, presence and extent of topographic barriers, proximity to other favorable habitats), nonhuman predation, and hunting activities of pre-European human populations (Truett 1996). Truett (1996) proposed that water scarcity and hunting by pre-European peoples were primary factors explaining low numbers of large ungulate herbivores encountered by early Europeans throughout much of the American Southwest. Archaeological findings suggest that small numbers of bison may have been present occasionally in some dryland locations on the Colorado Plateau during late-Holocene times (e.g., Mead et al. 1991). But overall, herbivory and trampling by large ungulates probably were relatively minor disturbances in most dryland ecosystems of the region during the period prior to European settlement.

5. Landscape-Level Relationships

This report has focused on functional relationships among components of dryland ecosystems, but for purposes of ecosystem management and monitoring it also is important to recognize functional relationships among ecosystems in landscapes (Wiens et al. 2002). A *landscape* is a spatially structured mosaic of different types of ecosystems interconnected by ecological flows of materials (e.g., water, sediments), energy, and organisms. Included in this definition is the notion that some of these flows may represent disturbances or stressors ([Fig. 8a](#)). A landscape perspective is essential for management and monitoring of bounded reserves such as NPS units where ecosystems within parks can be significantly affected by activities occurring well outside park boundaries. Consideration of landscape-level processes also can be important for assessing whether ecological conditions or events in one park location might generate ecological consequences elsewhere within the park (Reiners and Driese 2001).

Several aspects of landscape structure must be considered when assessing functional relationships among ecosystems in landscapes. These include ecosystem (or patch) type, ecosystem context, ecosystem condition, and ecosystem size (Groves et al. 2002, Wiens et al. 2002). Ecosystem *context* refers to the spatial configuration and connectivity of ecosystems ([Fig. 8](#)). Connectivity is the degree to which ecological flows can occur between ecosystems in a landscape. Connectivity depends on spatial configuration, but it also is strongly dependent on the process of interest and the degree of contrast between ecosystems. For example, two adjacent ecosystems may be connected hydrologically due to their location within a particular watershed, but differences in vegetation structure may cause the same two adjacent ecosystems to be disconnected with respect to the movement patterns of particular organisms or the transmission of disturbances such as fire. In this example, the degree of cross-boundary contrast does not affect hydrologic connectivity but it strongly affects boundary permeability to organisms and disturbance.
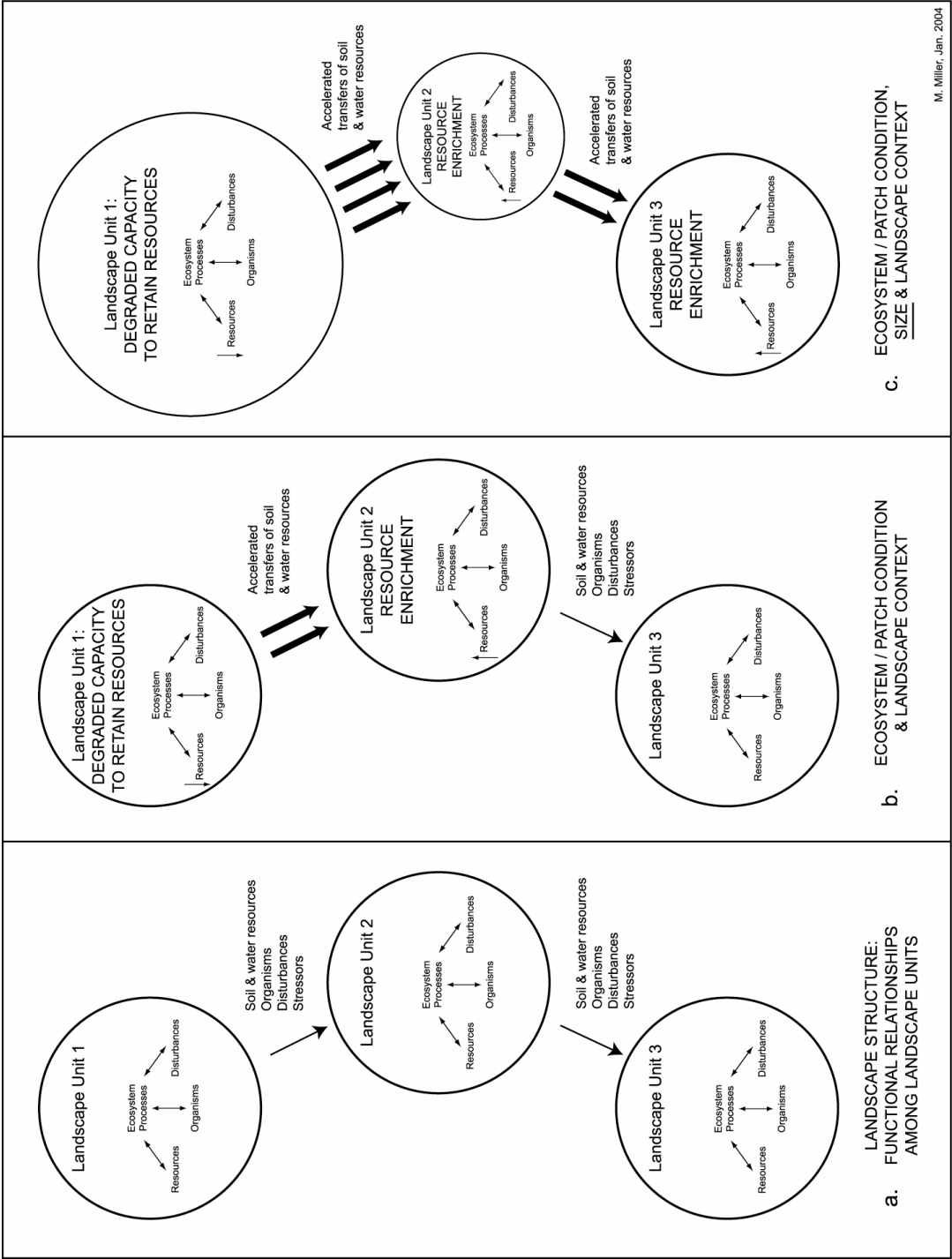
Figure 8. Examples of landscape-level processes and attributes important for ecosystem monitoring. In (a), landscape units are functionally connected by flows of soil and water resources, organisms, disturbances, and stressors. In (b), degraded conditions in Unit 1 are shown to cause resource enrichment in Unit 2 – illustrating the importance of landscape context. In (c), degraded conditions in Unit 1 are propagated to Unit 3 due to increased size of Unit 1 and decreased size of Unit 2.

From an ecosystem perspective, *condition* refers to the functioning of ecological processes required to sustain ecosystem characteristics including abiotic and biotic structure, productivity, rates of biogeochemical cycling, and natural disturbance regimes. The condition of ecosystems in the landscape can affect among-system flows and the ecological consequences of among-system flows. For example, a diminished capacity for soil and water retention in one ecosystem can result in accelerated resource transfers to connected ecosystems (Fig. 8b). Consequences of resource enrichment in the receiving ecosystem are dependent on conditions there. If invasive species are present in the receiving ecosystem, resource enrichment may result in rapid population expansion (Davis et al. 2000, With 2002). When considered with respect to individual species, ecosystem condition is equivalent to the notion of habitat quality (Wiens et al. 2002).

The meaning of ecosystem *size* is intuitive, and ecosystem size (or changes in ecosystem size) can affect the type, magnitude, and consequences of among-system flows (Fig. 8c). For ecosystem-level conservation targets characterized by large-scale disturbance regimes (e.g., extensive fire), it may be necessary to expand the notion of ecosystem size to encompass the amount of area required for the ecosystem to persist under the influence of characteristic large-scale disturbances. This area has been referred to as the *minimum dynamic area* (Pickett and Thompson 1978, Peters et al. 1997, Groves et al. 2002).

C. Predominant Anthropogenic Stressors

This section briefly describes predominant anthropogenic stressors affecting the structure and functioning of dryland ecosystems in SCPN and NCPN units. Additional information on the significance of these stressors in particular parks can be found in associated NPS reports (Evenden et al. 2002, Thomas et al. 2003, Miller et al. 2003). Details concerning potential ecological effects of these stressors are summarized in tabular format in Appendix B and in diagrammatic process models presented in the subsequent section of this report.

1. Visitor Use

Park use by terrestrial recreationists has been identified as a primary stressor of concern in many NCPN units and, to a lesser degree, in some SCPN units. Most parks experienced rapid growth in the number of annual recreational visits between the mid-1980s and the mid-1990s (Evenden et al. 2002, Thomas et al. 2003). These changes are exemplified by visitation patterns at CANY, which averaged 16 percent annual growth in visitation between 1985 and 1995. During the year 2000, CANY received seven times the number of recreational visits that it received in 1980. ZION – the most visited park in the NCPN – recorded over two million recreational visits in 2000, twice the number recorded in 1980. GRCA, consistently the most-visited SCPN park, has recorded over four million visitors every year since 1992 (Thomas et al. 2003). Potential resource impacts associated with terrestrial recreational activities include trampling of soils and vegetation (e.g., Cole 1990), dispersal of invasive exotic species, direct interactions with and disturbances of wildlife, and increased levels of water and air pollutants.

2. Livestock and Other Large Herbivores

Livestock use is permitted in portions of one SCPN park (GLCA) and four NCPN parks (DINO, CARE, CURE, and BLCA). Seasonal livestock trailing is permitted in FOBU and BRCA, and several other parks repeatedly experience trespass livestock. Most other parks were grazed by domestic livestock at one time, and many parks have on-going issues associated with persistent legacies of past livestock grazing and livestock-management practices. Herbivory and trampling by elk (BAND), bison (CARE and GRCA), and feral burros (GRCA) also occur. Potential ecosystem-level impacts of herbivory and trampling by large herbivores (particularly at levels exceeding natural regimes) were described above.

3. Fire Suppression

Ecological legacies of altered fire regimes are significant resource-management issues in many parks (Evenden et al. 2002, Thomas et al. 2003). Altered fire regimes attributable to past livestock grazing (fuel removal) and fire-suppression efforts have caused significant changes in vegetation structure and functioning of associated ecosystem processes. Mediated by changes in vegetation structure, ecosystem-level consequences of altered fire regimes can include diminished hydrologic functioning and increased erosion rates (e.g., Wilcox et al. 1996, Davenport et al. 1998, Jacobs and Gatewood 1999), as well as increased ecosystem susceptibility to drought and other disturbances and/or stressors.

4. Invasive Exotic Plants

Concern regarding the ecological impacts of invasive exotic plants is nearly uniform among SCPN and NCPN parks (Evenden et al. 2002, Thomas et al. 2003). Following are specific examples describing the extent of the invasive plant problem in dryland ecosystems of SCPN and NCPN parks:

- Approximately 24 percent of the total land area of GLCA may be infested with invasive plant species;
- Significant proportions of grasslands found in CANY and ARCH have been converted to dominance by cheatgrass (*Bromus tectorum*); and
- Cheatgrass constitutes approximately 85 percent of the dominant understory vegetation at YUHO.

Ecological effects of exotic species' invasions vary depending on the characteristics of the invader and the invaded ecosystem, but they can include major changes in community composition (Bock et al. 1986), competitive displacement of native species, and alterations of ecosystem-level properties such as disturbance regimes (D'Antonio and Vitousek 1992, Mack and D'Antonio 1998) and soil-resource regimes (Vitousek 1990, Evans et al. 2001). Many invasive plant species also possess physiological traits that will enable them to benefit from aspects of global change such as increased levels of atmospheric CO_2 and warmer minimum temperatures during winter (Alward et al. 1999, Dukes and Mooney 1999, Smith et al. 2000).

5. Adjacent Land-Use Activities

Ecological effects of adjacent land-use activities also represent a uniform concern among SCPN and NCPN units (Evenden et al. 2002, Thomas et al. 2003). Particular activities of concern include livestock grazing, forest management, urban/exurban development, and emissions of industrial and agricultural pollutants. Potential resource issues associated with adjacent land-use activities include altered habitat structure for wide-ranging wildlife species; increased transfers of soil and water resources; emissions of airborne and waterborne pollutants; introductions of exotic plant and animals species; diminished quality of soundscapes, nightskies, and viewsheds; and water diversion and/or regulation.

6. Air Pollutants

Air pollutants including particulates, tropospheric ozone, and nitrogen deposition are concerns at several SCPN and NCPN parks (Evenden et al. 2002, Thomas et al. 2003). Acid deposition may be an issue at MEVE (Romme et al. 2003b). Nitrogen deposition in particular has potential implications for numerous ecological patterns and processes including ecosystem susceptibility to exotic species invasions (Asner et al. 1997, Galloway et al. 2003, Fenn et al. 2003b). Although current rates of N deposition generally are low across most of the western United States, there is very little information available for areas immediately downwind of emissions sources (Fenn et al. 2003a,b). Notably, modeling indicates potential "hot spots" of N deposition in the vicinity of MEVE and ZION (Fenn et al. 2003a).

7. Global Atmospheric Changes

Global atmospheric changes attributable to anthropogenic emissions of CO_2 and other greenhouse gases are expected to have significant environmental consequences during this century (Houghton et al. 2001). Increasing levels of atmospheric CO_2, increasing soil and air temperatures, and altered precipitation patterns (including a potential increase in the frequency of extreme events) are likely to affect physiological processes and competitive relations of vascular plants, nutrient cycles, hydrologic processes, and disturbance regimes – all of which have the potential to greatly alter the structure and functioning of dryland ecosystems (e.g., Alward et al. 1999, Ehleringer et al. 2000, Smith et al. 2000, Weltzin et al. 2003) and the sensitivity of these systems to other anthropogenic stressors. Despite modeling efforts, there is great uncertainty about how global atmospheric changes will affect temperature and precipitation patterns in particular regions such as the Colorado Plateau. Uncertainty regarding regional climatic consequences and ecological outcomes of global-change processes greatly compound the challenges associated with ecosystem management and monitoring

III. ECOSYSTEM DYNAMICS

In this section, conceptual models are presented to describe hypotheses about how and why dryland ecosystems change through time. These models do not describe characteristic natural dynamics of the

many specific dryland ecosystems found in the region. Instead, they emphasize dynamics associated with a very generalized set of processes and pathways of degradation[7] that have been described for dryland ecosystems. The models are intended to depict general ways in which natural drivers (e.g., climate and disturbance) interact with stressors and/or management actions to affect the likelihood of these degradational changes. Because of the generalized nature of these models, they will require refinement for application to specific ecosystems on a site-specific basis. Following the models, this section ends with a brief discussion of factors affecting the susceptibility of dryland ecosystems to change.

A. Background – Alternative Ecosystem States

Sustainable ecosystems, as defined by Chapin and colleagues (1996), are persistent. Through the typical pattern of dynamics driven by disturbance events and climatic fluctuations, such ecosystems maintain their characteristic diversity of major functional groups, productivity, and rates of biogeochemical cycling (Chapin et al. 1996). Inherent in the notions of ecosystem sustainability and persistence is the hypothesis that ecosystems can be caused to transition from one state to an alternative state. Though capable of existing in the same physical location, these alternative ecosystem states are distinguished by relatively large differences in structure and in rates of ecological processes such as erosion, nutrient cycling and disturbance regime. Such differences in structure and processes typically are matched by great differences in ecosystem dynamics. A transition from one state to an alternative state may occur gradually or relatively rapidly as the result of natural processes (e.g., climatic disturbances) or human actions (e.g., land-use activities). Frequently, human actions and natural processes interact to cause persistent transitions among states (Westoby et al. 1989, Bestelmeyer et al. 2003, Stringham et al. 2003, Bestelmeyer et al. 2004).

Of greatest concern from a conservation perspective are alternative ecosystem states that reflect a degraded capacity to perform desired ecosystem functions. Ecosystems that have been driven across thresholds of degradation cannot be restored to previous conditions simply by removing the stressor. Costly, manipulative restoration efforts are required (Hobbs and Norton 1996, Whisenant 1999, Suding et al. 2004). The success of such restoration efforts usually is uncertain, and in some cases restoration may be impractical due to financial and technical constraints. Dryland ecosystems and aquatic ecosystems are the most-frequently cited examples of systems characterized by multiple alternative states (Rapport and Whitford 1999, Whitford 2002, Scheffer and Carpenter 2003).

B. Common Pathways and Processes of Dryland Degradation

The conceptual framework of alternative states is a useful one for identifying monitoring needs associated with the goal of sustaining the integrity[8] of park ecosystems. This alternative-state framework is depicted graphically in Figure 9. In this framework, the desired state (State A) is represented by a dynamic ecosystem in which the characteristic abiotic and biotic components and processes are present and functioning within the natural range of variability, including processes that confer ecosystem resistance and resilience to natural disturbances and anthropogenic stressors. However, as a consequence of on-going global-change processes (e.g., altered atmospheric chemistry, temperatures, and precipitation patterns), managers should recognize that future ecosystem characteristics are likely to drift away from historic patterns of variability. Accordingly, the concept of the "desired state" will have to account for uncertain trajectories of global atmospheric change (e.g., Currie 2001, Shafer et al. 2001, Hannah et al. 2002, Walther et al. 2002) as well as factors such as altered landscape configurations and the introduction of invasive exotic species to regional and local species pools.

Despite uncertainties associated with future trajectories of change, four commonly-observed types of degraded states remain pertinent for purposes of ecosystem management and monitoring (Fig. 9, boxes B through E). These are described here as follows:

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[7] For purposes of this report, _degradation_ is defined as an anthropogenic reduction in the capacity of a particular ecosystem or ecosystem component to perform desired functions such as the conservation of soil and water resources or the maintenance of native biodiversity. Degradation also can be interpreted as an anthropogenic reduction in the capacity of a system to maintain itself within the range of desired conditions specified by ecosystem managers.

[8] _Ecological integrity_ is a concept that expresses the degree to which the physical, chemical, and biological components (including composition, structure, and process) of an ecosystem and their relationships are present, functioning, and capable of self-renewal (http://science.nature.nps.gov/im/monitor/Glossary.htm).
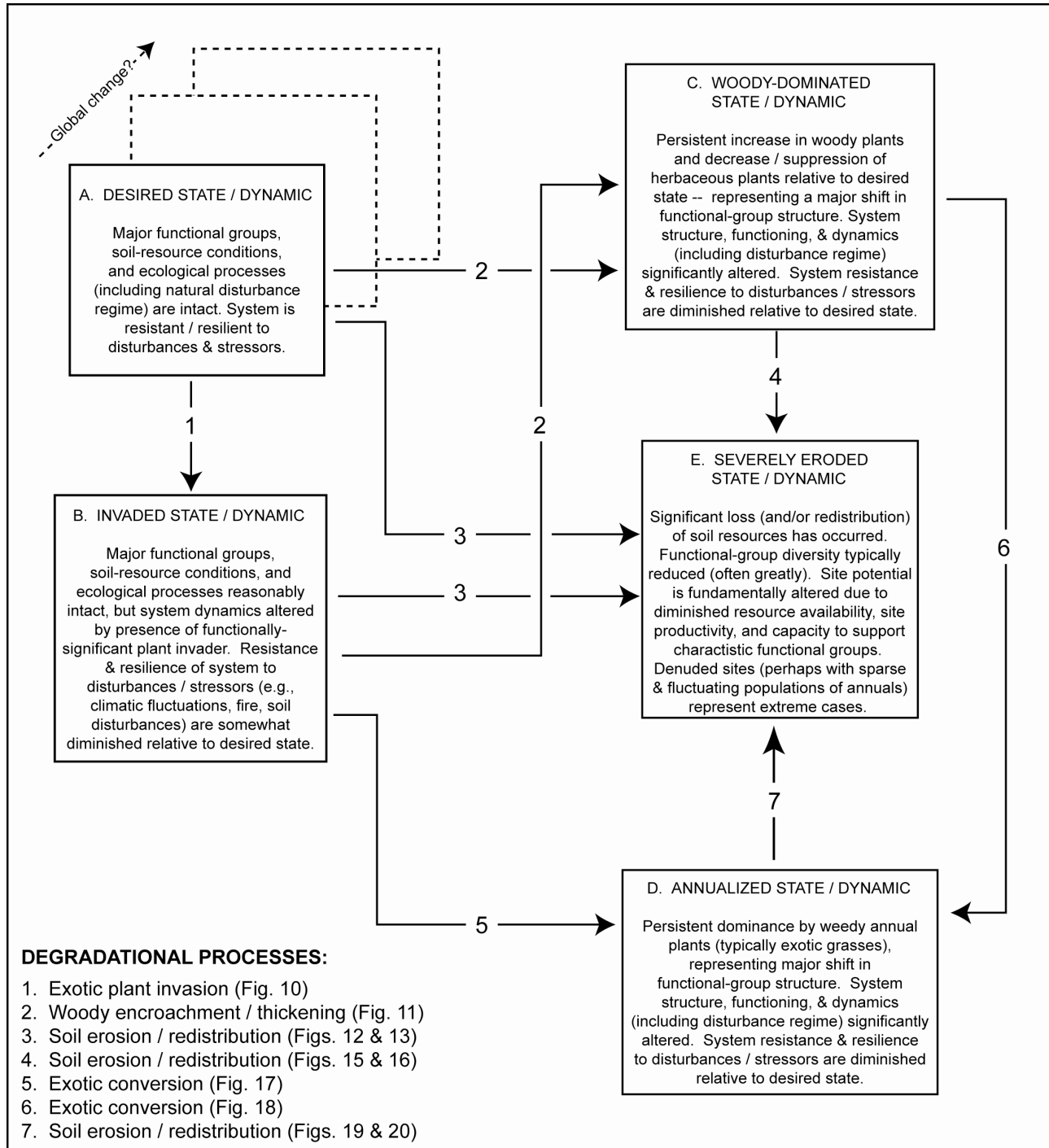
Figure 9. Conceptual model depicting major types of degraded alternative states (boxes B through E) that characterize dryland ecosystems of the region. Numbered arrows reflect general ecological processes responsible for transitions among states (see accompanying figures for detailed process models). Although not shown here, each state is characterized by a typical pattern of dynamic behaviour. For State A, that pattern of behaviour encompasses the "natural range of variability." Dashed boxes associated with State A reflect the likelihood that global-change processes (e.g., altered atmospheric chemistry, temperatures and precipitation) will cause future patterns of variability to drift away from historic patterns.

- The invaded state (State B) – characterized by the presence of a functionally significant invasive exotic plant (e.g., *Bromus tectorum*). System structure and functioning are somewhat altered relative to the desired state, but major functional groups and associated ecosystem processes generally remain intact. Presence of the invader may affect ecosystem resistance or resilience to natural disturbances or anthropogenic stressors.
- The woody-dominated state (State C) – characterized by a persistent increase in the ratio of woody plant biomass to herbaceous plant biomass relative to the desired state. Associated with this major structural change, ecosystem functioning (e.g., disturbance regimes, rates of geomorphic and biogeochemical processes) also are significantly altered relative to the desired state.
- The annualized state (State D) – characterized by persistent ecosystem dominance by weedy annual plants – often including invasive exotics species such as *Bromus tectorum*. Associated with this major structural change, ecosystem functioning (e.g., disturbance regimes, rates of geomorphic and biogeochemical processes) also are significantly altered relative to the desired state.
- The severely eroded state (State E) – characterized by severe loss or redistribution of soil resources. Site conditions have been fundamentally altered due to diminished (or persistently redistributed) resource availability, site productivity, and site capacity for supporting biotic functional groups characteristic of State A.

Depending on site-specific properties of particular ecosystems, there may be numerous expressions and intergradations of these four basic types of degraded states. In addition, there is tremendous variability among particular sites in their susceptibility to various transitions depicted in Figure 9. Transition susceptibility varies as a function of (1) *ecosystem exposure* to driving processes, and (2) *ecosystem resistance and resilience* to driving processes. These factors are discussed briefly at the end of this section.

Following are conceptual models describing degradational processes associated with transitions depicted in Figure 9. As with Figure 9, these process-based models are necessarily generalized and will require modification for site-specific applications. The relative significance of processes depicted in the models can be expected to vary widely among sites. The models are intended to assist managers in the consideration of ecosystem attributes to be included in a long-term monitoring program designed to support the conservation of park resources. The models are not meant to imply that ecosystem degradation is the certain outcome of particular factors or processes.

1. Transition 1 – Exotic Plant Invasion

The transition from the desired state to the invaded state is caused by the establishment and spread of a functionally significant plant invader. Propagule dispersal clearly is an important factor in this transition, but resources also must be available if the introduced population is to reach a size sufficient for it to affect ecosystem functioning. Davis and colleagues (2000) recently proposed a simple conceptual model illustrating their well-supported hypothesis that an ecosystem becomes more susceptible to invasion when there is an increase in the amount of resources that otherwise limit invasion (Fig. 10). Factors that cause a pulse in resource supply (e.g., precipitation events or fire) or a reduction in resource uptake (e.g., episodic mortality of community dominants) may enable the rapid population expansion of responsive invaders that previously existed in the ecosystem at low levels. Other workers also have emphasized the importance of temporal and spatial patterns of resource availability as factors affecting ecosystem susceptibility to invasion (Johnstone 1986, With 2002). Consistent with the resource-based hypothesis of Davis and colleagues, there is increasing evidence that ecosystems or microsites that are rich in soil resources are particularly susceptible to invasion by exotic species (Stohlgren et al. 1999, Levine and D'Antonio 1999, Búrquez-Montijo et al. 2002).
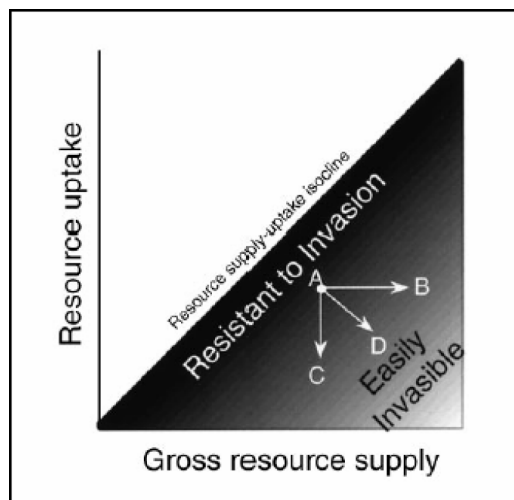
Figure 10. Conceptual model illustrating the hypothesis that an ecosystem becomes more susceptible to invasion when there is an increase in the amount of resources that otherwise limit invasion. Resource availability can increase due to a pulse in supply (A→B), a reduction in resource uptake (A→C), or both (A→D) (from Davis et al. 2000).

For example, the pulsed population expansion of *Bromus tectorum* in a relatively undisturbed grassland in Canyonlands National Park was attributed to enhanced soil-moisture conditions resulting from an El Niño episode (Belnap and Phillips 2001). Subsequent to this population expansion, community dynamics in relation to interannual climatic fluctuations were substantially different than prior to the event. In experimental studies, Smith and colleagues (2000) found that the presence of the exotic annual grass red brome (*Bromus madritensis* subsp. *rubens*) in an otherwise intact Mojave Desert ecosystem affected ecosystem response to elevated concentrations of atmospheric CO_2. Similarly, the presence of invasive exotic plants can significantly degrade the resilience of dryland ecosystems to wildfire (Brooks et al. 2004) – thereby increasing the likelihood of a subsequent transition to a state dominated by an invader which promotes recurring fire (e.g., Transition 5 and State D in Fig. 9).

2. Transition 2 – Woody Plant Encroachment / Thickening

A persistent increase in the relative dominance of woody vegetation is perhaps the most widely documented transition in dryland ecosystems around the world (Archer 1994, Archer and Stokes 2000, http://rangeweb.tamu.edu/archer/bibliography.htm). Factors proposed most commonly as explanatory mechanisms include excessive grazing (and associated trampling) by domestic livestock, active fire-suppression efforts, and climate (Fig. 11). Elevated atmospheric CO_2 also has been suggested as a factor (Polley et al. 1996, 1997), although Archer and colleagues (1995) argued that CO_2 enrichment is an insufficient explanation for observed patterns of vegetation dynamics. Climate plays an important role due to effects on population dynamics and competitive relations of herbaceous versus woody plants, but persistent overgrazing by domestic livestock generally has been implicated as the most important driver of transitions involving increasing dominance of unpalatable woody plants (Archer et al. 1995, Van Auken 2000). Selective herbivory affects the competitive relations of plants, favoring the establishment and growth of unpalatable plants over those of palatable plants (Briske and Richards 1994). The reduction of above-ground herbaceous biomass and litter by grazing also reduces the availability of fine fuels required to support a regime of frequent surface fires. Where such a fire regime is important for constraining the dominance of fire-intolerant woody vegetation, the removal of fine fuels by grazing may be more important than reduced herbaceous competition or active fire-suppression efforts as a driver of ecosystem change (Archer 1994, Archer et al. 1995, Van Auken 2000).

Figure 11. Conceptual model illustrating the processes by which excessive grazing, fire suppression, and climate interactively lead to increasing dominance by woody plants.

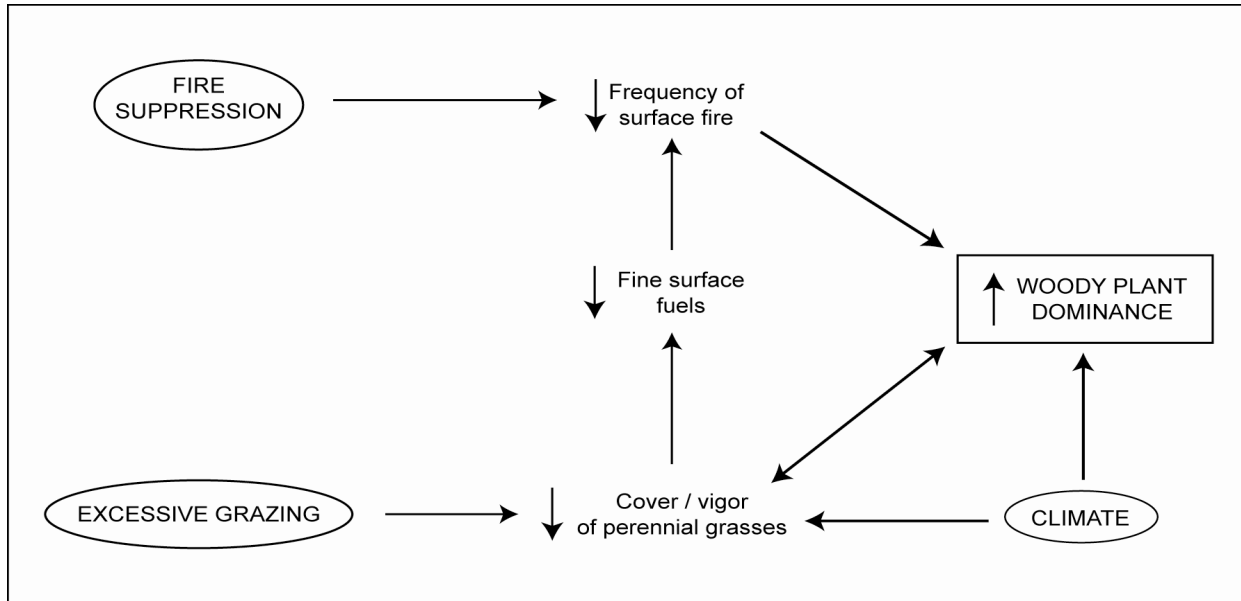In this region, examples of persistent woody transitions outside the range of natural variability include juniper encroachment in grasslands of northern Arizona (Johnsen 1962, Jameson 1962) and thickening of juniper and piñon in grasslands and savannas of north-central New Mexico (e.g., BAND; Allen 1989). These examples correspond with the piñon-juniper grass savanna ecosystem (*sensu* Romme et al. 2003a, Table 3), which is characterized by a natural disturbance regime of frequent, low-severity surface fires. This model also may apply to former sagebrush steppe ecosystems and piñon-juniper shrub woodlands (Romme et al. 2003a; Table 3) where land-use activities have altered ecosystem structure, lengthened fire-return intervals, and increased the range-wide proportion of systems that are shrub- or tree-dominated (Connelly et al 2004). In some circumstances, transition to this woody-dominated state may increase the likelihood of subsequent transitions to eroded or annualized states (i.e., Transitions 4 and 6 to States E and D in Fig. 9). It is important to recognize that this model does not apply to piñon-juniper forest ecosystems found at MEVE (Romme et al. 2003) and possibly elsewhere. Nor does it apply to sparse desert shrublands or semidesert grasslands referred to as galleta – three-awn shrub steppe.

Although human land-use activities frequently are implicated as primary drivers of woody transitions, it is important to recognize that increases in the relative dominance of woody vegetation also can occur in the absence of such activities. Between 1958 and 1996, juniper and piñon increased in sagebrush shrublands on a remote mesa in Grand Canyon National Park that was unimpacted by human land-use activities (Rowlands and Brian 2001). Similarly, Harris and colleagues (2003) found a significant increase in the dominance of woody vegetation on an ungrazed mesa in southern Utah between 1948 and 1993. In both cases, increases in the dominance of woody vegetation appear to be driven by natural successional processes. As indicated previously, area-specific research is necessary to evaluate natural disturbance regimes and processes responsible for observed dynamics.

3. Transition 3 – Soil Erosion / Redistribution

Transition 3 (Fig. 9) is associated with accelerated erosional processes that result in a significant and persistent decline in soil-resource availability, site productivity, and site capacity for supporting biotic functional groups characteristic of the desired state. Soil resources can be eroded and redistributed by aeolian processes (Fig. 12), fluvial processes (Fig. 13), or both. Whether wind or water is the driving force, factors leading to accelerated rates of soil erosion and redistribution are similar. Trampling and other soil-surface disturbances can diminish soil stability by damaging biological soil crusts that protect and retain soils against erosive forces of wind, rain, and runoff (Williams 1995a; Belnap and Gillette 1998, Okin et al. 2001). Soil-surface disturbances also can disrupt stable soil aggregates that enhance soil stability and soil infiltration capacity (Thurow 1991). By reducing herbaceous cover and organic-matter inputs from litter and

roots, excessive grazing can diminish soil protection and soil aggregate stability (Thurow 1991). Reductions in vegetative ground cover also can result in accelerated erosion due to diminished capacity to obstruct wind and overland flow of water (Davenport et al. 1998, Reid et al. 1999, Ludwig and Tongway 2000). Because of the complex and poorly understood effects of biological soil crusts on hydrologic processes (described above), in Figure 13 some uncertainty is indicated regarding effects of biological soil crusts on water and sediment capture and retention. Off-site conditions (i.e., the functional status of adjacent landscape units; Fig. 8) can contribute to accelerated rates of erosion due to effects of saltating soil particles on aeolian soil detachment (Fig. 12; Toy et al. 2002) and effects of runoff on fluvial soil detachment and transport (Fig. 13; Thurow 1991). Climate plays a role in this transition due to effects on vegetative ground cover and the frequency of erosive wind and precipitation events (e.g., Fig. 5). As soil resources are lost due to erosional processes, declining resource availability generates a positive feedback facilitating further declines in vegetative ground cover and further increases in erosion (Figs. 12 and 13; e.g., Tongway et al. 2003, Friedel et al. 2003, Sparrow et al. 2003).

In the Colorado Plateau region, good examples of this transition can be found on stream-terrace soils that have been impacted by soil-surface disturbances (Fig. 14). In this landscape setting, a typical intact soil profile consists of a thin (0-5 cm) surface horizon of fine sandy-loam texture that overlies a thick sub-surface argillic (clay-rich) horizon with high sodium content caused by capillary rise of alluvial groundwater (e.g., the Elias series – for description see http://ortho.ftw.nrcs.usda.gov/cgi-bin/osd/osdname.cgi). Where unimpacted by land-use activities, such sites are generally characterized by well-developed biological soil crust communities, productive stands of the C_4 bunchgrass *Sporobolus airoides* (alkali sacaton), and the shrub *Sarcobatus vermiculatus* (greasewood). Destabilization and loss of the surface horizon exposes a horizon with physical and chemical properties that tend to inhibit establishment of vascular plants and biological soil crusts, as well as enhance runoff and water-driven erosional processes. In all cases where this occurs, ecosystem structure and functioning are persistently altered; in extreme cases, erosion leads to the development of badland topography. Examples similar to those depicted in Figure 14 can be found in CARE.

4. Transition 4 – Soil Erosion / Redistribution

Erosional processes associated with Transition 4 (Figs. 15 & 16) are similar to those associated with Transition 3 (Figs. 12 & 13), but in the former case processes are modified due to an increase in the dominance of woody vegetation compared with the desired state. Relative to Transition 3, within-site soil redistribution is more important in Transition 4 (Figs. 15 & 16). Soil resources transported from interspaces may be captured and retained within the sub-canopy environments of woody plants due to interactions of shrubs and trees with wind- and water-driven geomorphic processes. The redistribution of soil resources from intercanopy spaces to sub-canopy environments contributes to a positive feedback favoring continued increases in the ratio of woody to herbaceous biomass. Regional examples of the positive-feedback linkage between soil redistribution and increasing dominance of woody vegetation include coppiced shrublands of Monument Valley (pers. obs.) and piñon-juniper rocklands of BAND where severe erosion has been facilitated by past grazing and fire-regime alterations that led to increased tree cover and diminished herbaceous cover (Allen 1989, Wilcox et al. 1996, Davenport et al. 1998, Jacobs and Gatewood 1999). This positive-feedback model has been proposed as a common pathway of dryland degradation or "desertification" (Schlesinger et al. 1990, Havstad et al. 2000).

Figure 12. Conceptual model illustrating the processes by which excessive grazing, soil-surface disturbances, off-site soil-surface disturbances, and climate interactively lead to the erosion / redistribution of soil resources by wind.

Figure 13. Conceptual model illustrating the processes by which excessive grazing, soil-surface disturbances, off-site hydrologic dysfunction, and climate interactively lead to the erosion / redistribution of soil resources by water.
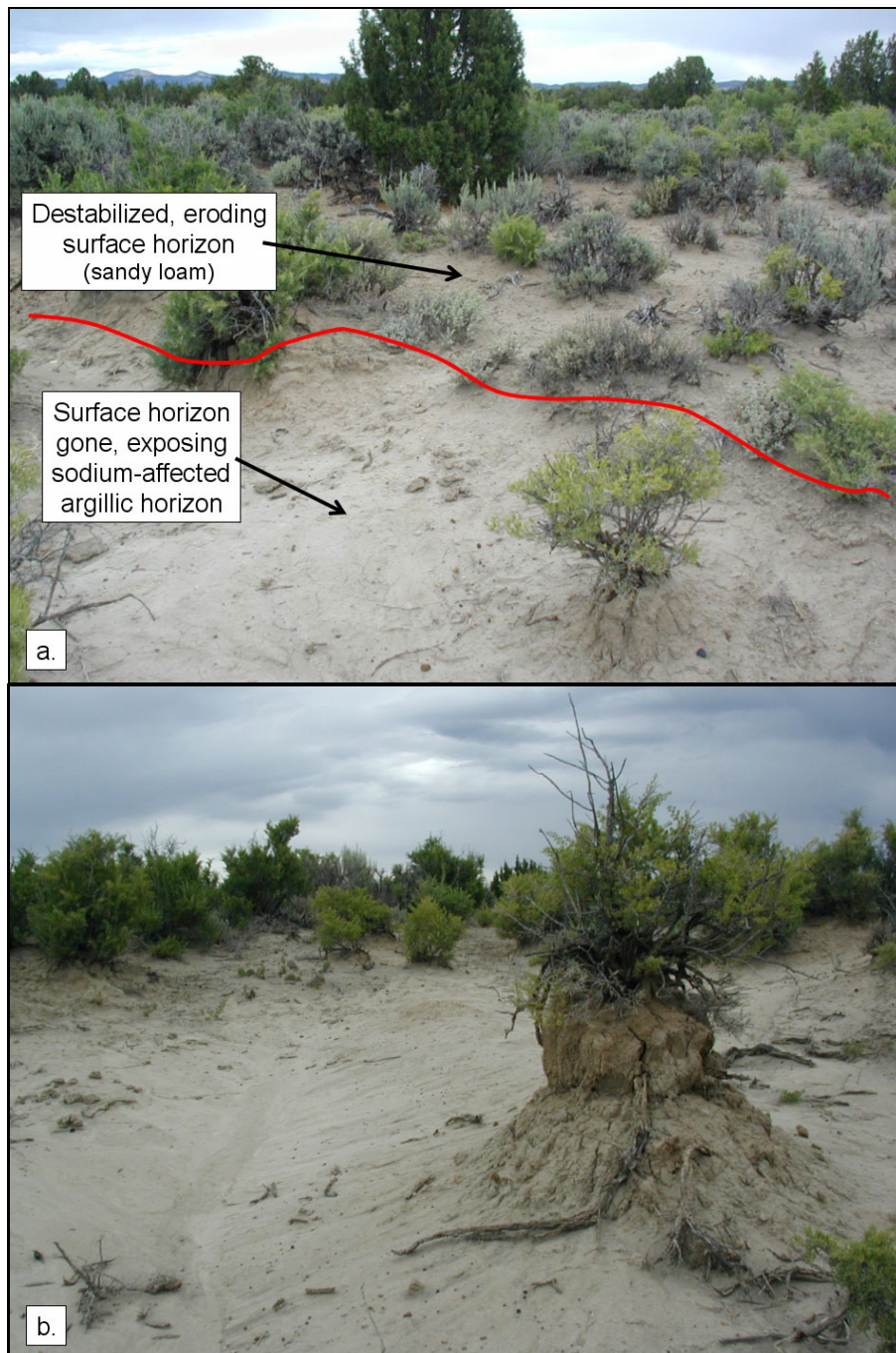
Figure 14. Example of site where accelerated erosion has led to the significant loss of soil resources and persistent alteration of ecosystem structure and functioning. In (a), the area above the red line retains a sandy-loam surface horizon that, though unstable and eroding, facilitates water infiltration and provides conditions suitable for vascular-plant establishment. Where this thin surface horizon has been lost below the red line, soil physical and chemical properties inhibit plant establishment and facilitate water-driven erosion. Panel (b) illustrates extreme results of erosion at this site. Photographs are of a site in Headquarters Valley, Grand Staircase-Escalante National Monument, Utah. Soil is transitional between an Elias series (Natriargid) and a Barx series (Calciargid) (Kent Sutcliffe, pers. commun.).

Figure 15 Conceptual model illustrating the processes by which increasing woody-plant dominance, excessive grazing, soil-surface disturbances, off-site soil disturbances, and climate interactively lead to the erosion / redistribution of soil resources by wind.

Figure 16. Conceptual model illustrating the processes by which increasing woody-plant dominance, excessive grazing, soil-surface disturbances, off-site hydrologic dysfunction, and climate interactively lead to the erosion / redistribution of soil resources by water.

5. Transition 5 – Exotic Conversion

The persistent conversion of dryland ecosystems to dominance by exotic annuals is a widespread pathway of degradation (e.g., Billings 1990, Connelly et al. 2004). Many weedy annuals may be involved, but exotic annual grasses are the most common dominants. Several factors may contribute to processes associated with this transition to an "annualized" state (Fig. 17), but all of them invariably affect the availability of resources that otherwise limit population growth in the exotic species (Davis et al. 2000; Fig. 10). In this context, resources may include safe sites for germination and establishment (Harper 1977, Grubb 1977), as well as water, mineral nutrients, and light. Soil-surface disturbances may facilitate establishment of ruderal exotic species if availability of safe-site opportunities is a limiting factor (Crawley 1987). However, if soil-surface disturbances do not ameliorate resource limitations, then soil-surface disturbance alone will not facilitate a transition to exotic dominance (Hobbs 1991). Excessive grazing can reduce the competitive abilities of native perennial grasses relative to exotic annuals if the former are preferentially grazed, thereby favoring population expansion of lesser grazed exotic annuals. Resource enrichment associated with climatic episodes, fire, resource transfers from adjacent sites, excreta from localized livestock concentrations, or atmospheric N deposition may facilitate population expansion and persistent conversion to dominance by exotic annuals – particularly if these factors simultaneously have an adverse effect on native competitors (e.g., livestock grazing). Increasing dominance by exotic annuals can lead to a dramatic shift in fire regime where annuals drive increases in the abundance and continuity of fine fuels and in the frequency of surface fires (Brooks et al. 2004). Although a shift in fire regime does not always accompany ecosystem annualization, the positive-feedback linkage between exotic grasses and wildfire is sufficiently widespread to have been proposed as an important element of global change (D'Antonio and Vitousek 1992). Fenn and colleagues (2003b) suggested that, in some locations, atmospheric N deposition could trigger fire – exotic grass cycles by increasing resource availability for exotics. Experimental results from the Mojave Desert suggest that increasing levels of atmospheric CO_2 may have a similar triggering effect (Smith et al. 2000). Romme and colleagues (2003b) expressed concern that invasive exotic species could respond to natural fires in piñon-juniper ecosystems of MEVE and subsequently initiate a fire – exotic species cycle. Examples of annualized ecosystems occur in several NPS units in the Colorado Plateau region, including CANY, ARCH, GOSP, ZION, and CARE. In some circumstances, annualization may accelerate erosional processes that lead to further site degradation (e.g., Transition 7 to State E in Fig. 9).

6. Transition 6 – Exotic Conversion

Similar to the concerns of Romme and colleagues (2003b) regarding the potential for exotic conversion following wildfire in MEVE ecosystems, West (1999) suggested that persistent increases in the dominance of woody vegetation could facilitate exotic conversion by increasing the likelihood of high-intensity fires (Fig. 18). Due to increased levels of competition, unnaturally dense populations of woody plants also may be more susceptible to drought, insect infestations, or other disturbances / stressors. Whether triggered by fire or some other factor, the sudden pulse of resources could enable rapid expansion of existing exotic-species populations. If the population expansion is sufficient to cause a persistent increase in the abundance and continuity of surface fuels, a self-maintaining fire–exotic species cycle could be initiated. This type of transition may be a concern in parks such as BAND where the early 21st century drought has triggered near-complete mortality in unnaturally dense piñon stands.
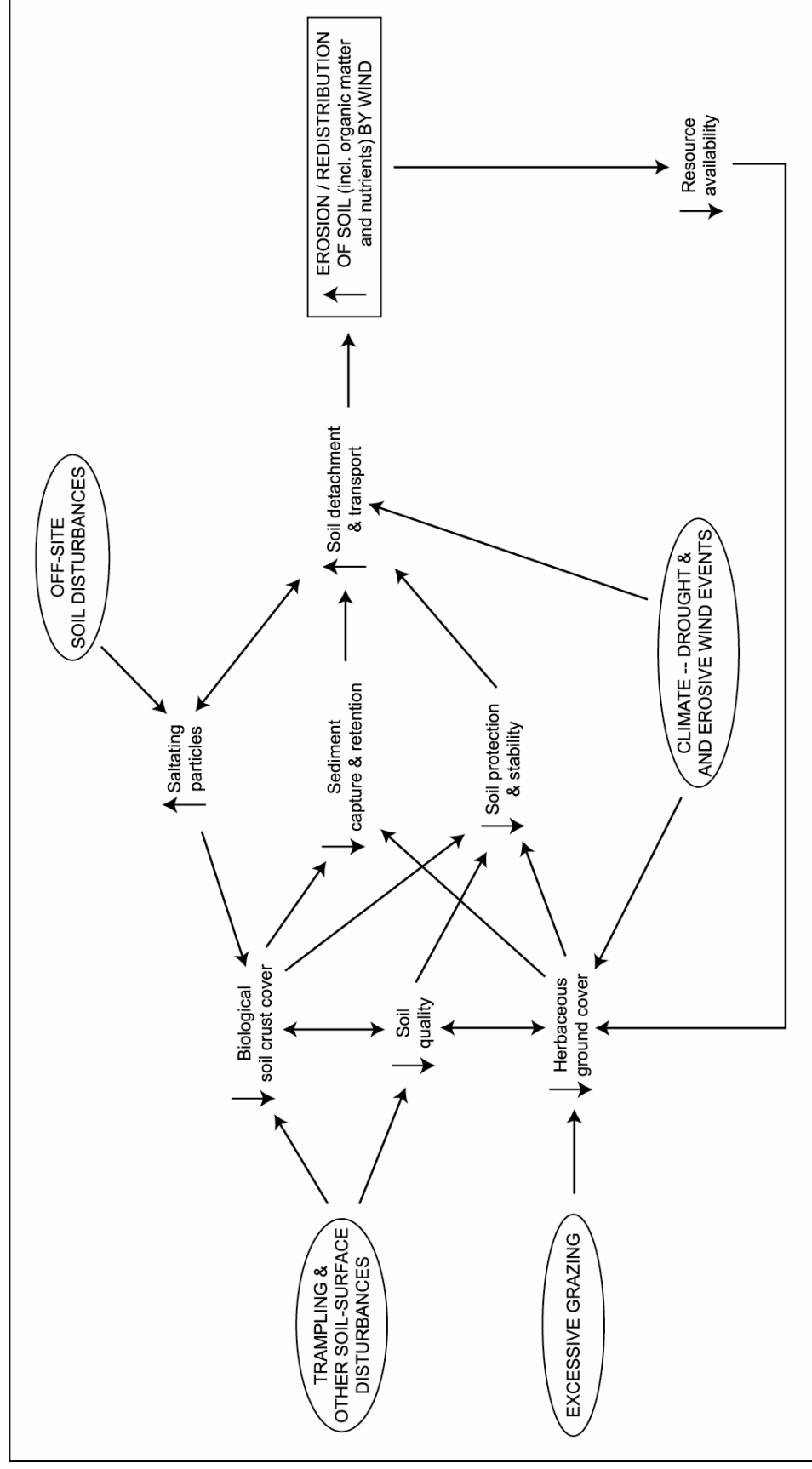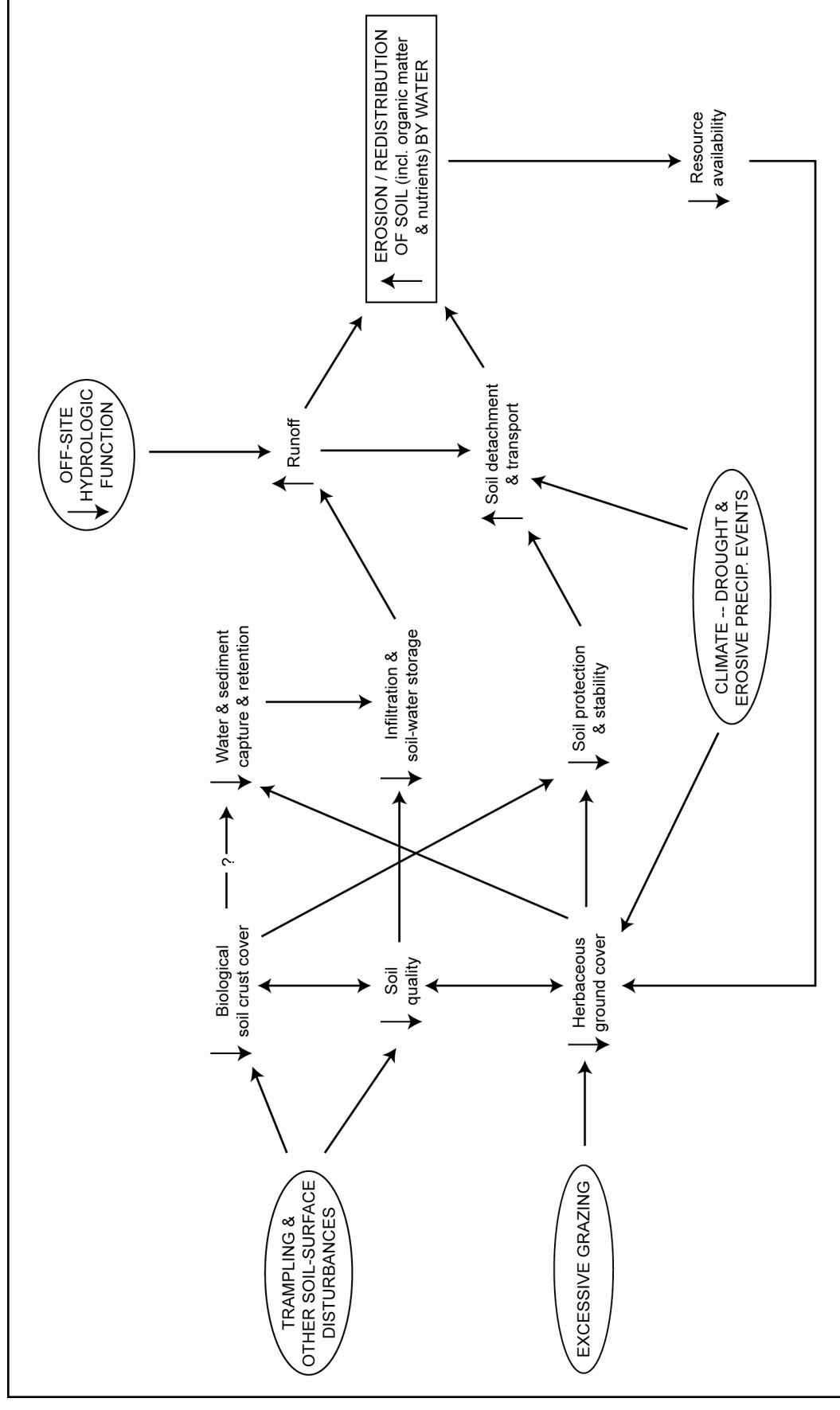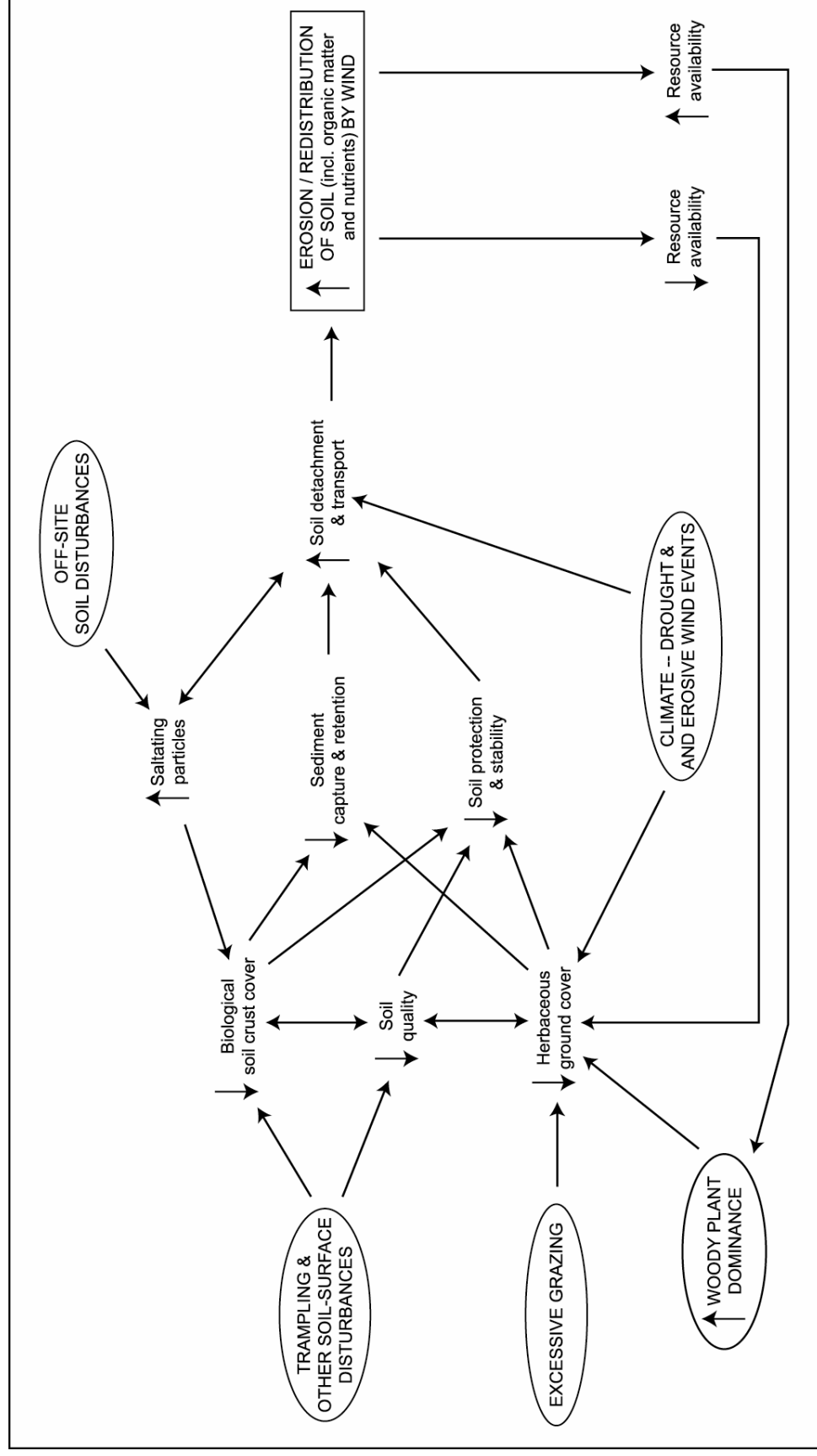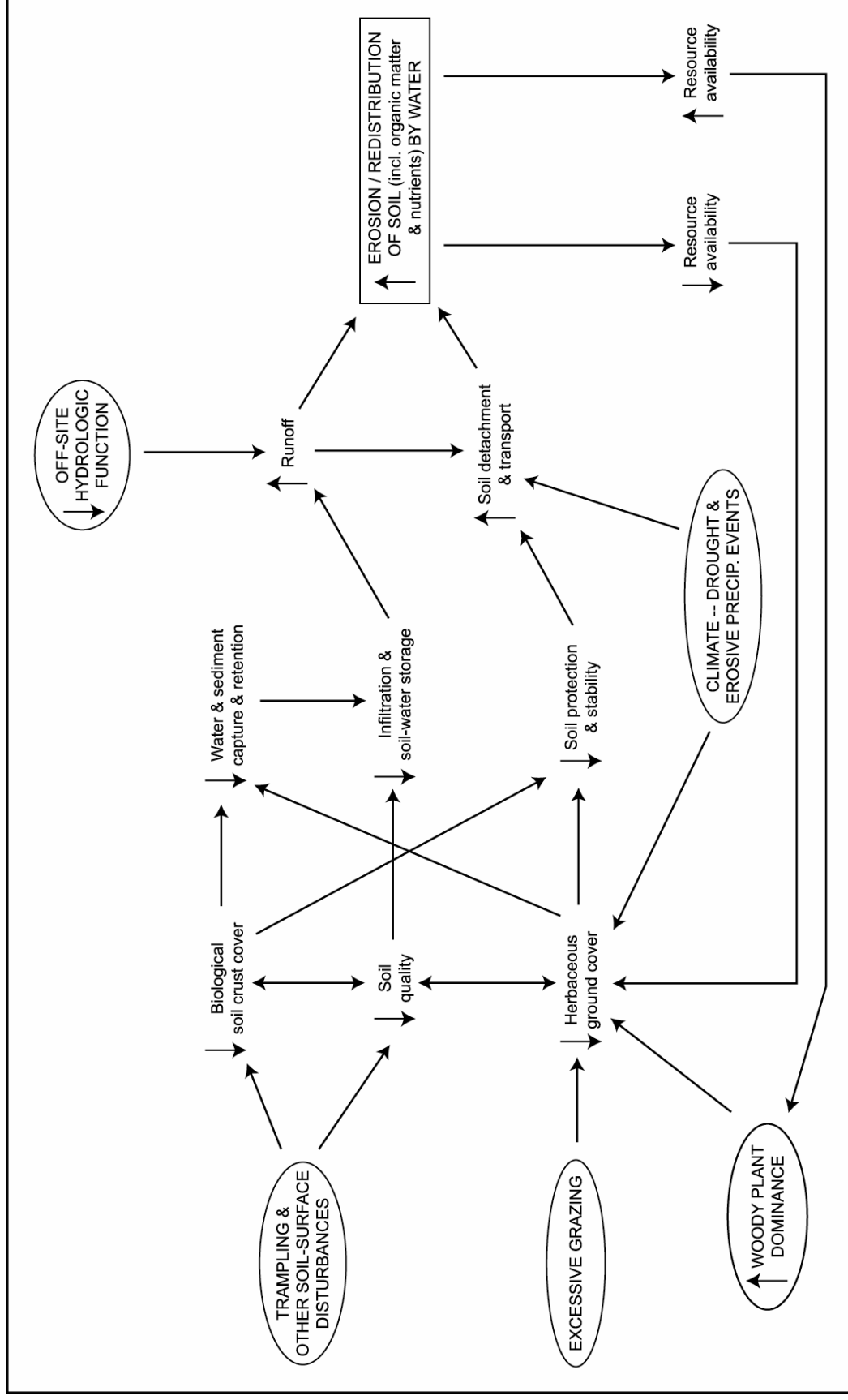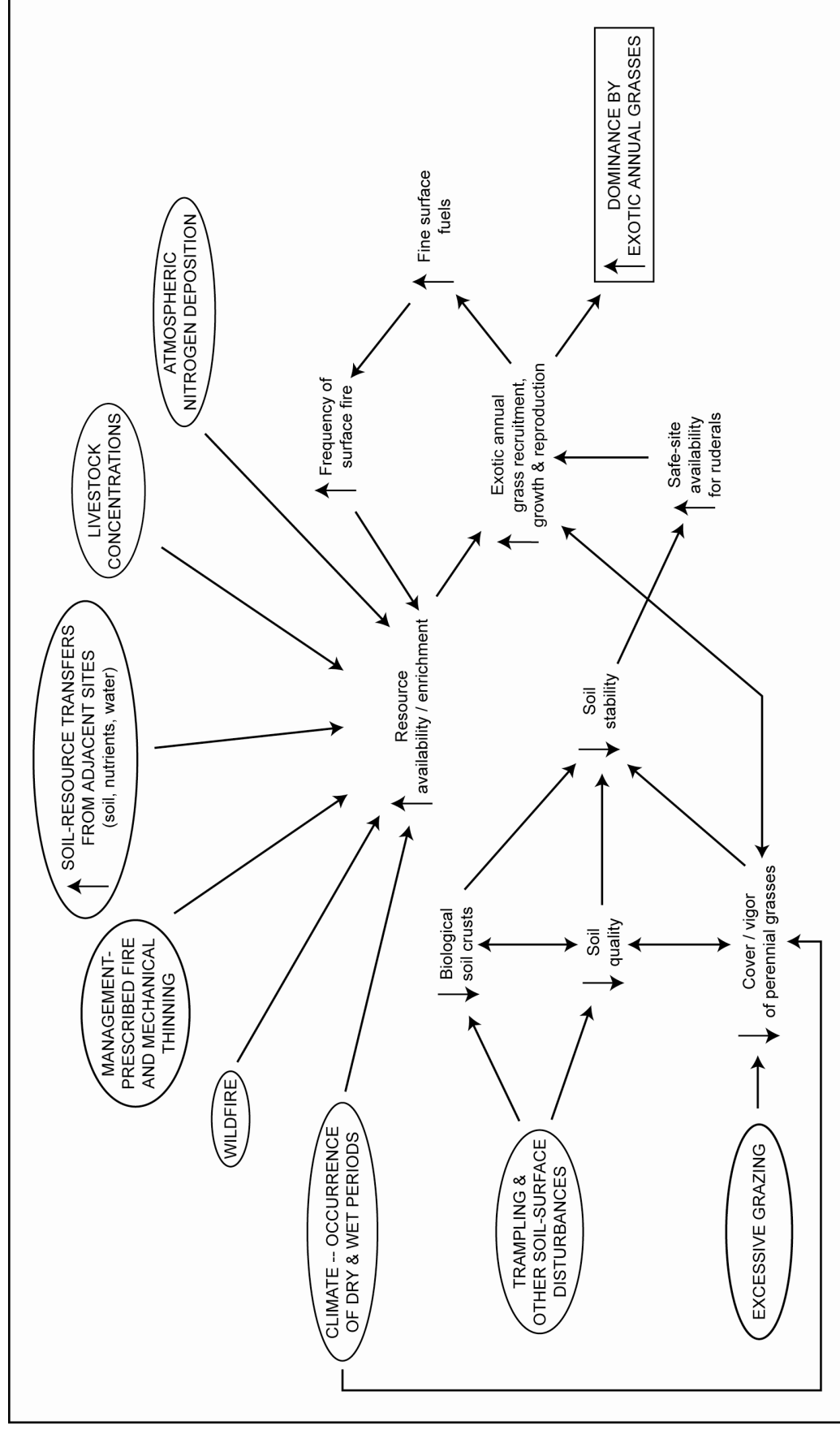
Figure 17. Conceptual model illustrating the processes by which excessive grazing, soil-surface disturbances, management-prescribed fire and mechanical thinning, wildfire, atmospheric nitrogen deposition, concentrated livestock activites, landscape-level soil-resource transfers, and climate interactively lead to increasing dominance (and site conversion) by exotic annual grasses.

7. Transition 7 – Soil Erosion / Redistribution

Severe erosion (transition to State E in Fig. 9) may be more likely in ecosystems dominated by exotic annual plants than in ecosystems dominated by perennial species because of greater fluctuations in annual ground cover in relation to climate (Figs. 19 and 20). Greater soil exposure to erosive forces during unfavorable periods could trigger spiraling processes of degradation as soil losses cause decreased ground cover and even greater soil exposure to erosive forces. Examples of eroding annualized ecosystems can be found in ARCH (Fig. 21) and CANY.

C. Ecosystem Susceptibility to Change

As indicated above, there is much variability among dryland ecosystems in their susceptibility to transitions depicted in Figure 9. Transition susceptibility varies as a function of (1) *ecosystem exposure* to driving processes, and (2) *ecosystem resistance and resilience* to driving processes. Depending on the goals and objectives of a long-term monitoring program, factors affecting ecosystem exposure, resistance, and resilience may play a role in spatial and temporal aspects of the monitoring design.

1. Ecosystem Exposure

Ecosystem exposure to drivers of change – particularly those considered to be anthropogenic stressors – is an important factor influencing ecosystem susceptibility to change beyond the range of conditions represented by the desired state. For example, sites exposed to frequent soil-surface disturbances or herbivory by large mammals will be more susceptible to transitions affected by those processes than sites that are not so exposed, all else being equal. Landscape configuration also must be considered when evaluating ecosystem exposure where stressors may be associated with ecological flows from connected landscape units (Fig. 8). At a regional scale, there is variation in ecosystem exposure to climatic factors (e.g., erosive, high-intensity precipitation events) that affect the probability of transitions caused by erosional processes (Fig. 6). Ecosystem exposure is not a static property. It can change with changes in climate and atmospheric conditions, landscape configuration, management, spatiotemporal properties or magnitude of existing stressors, or with the emergence of novel stressors.

2. Ecosystem Resistance and Resilience

Persistent transitions to degraded states occur when ecosystem properties that confer resistance and resilience are damaged or otherwise exceeded (Archer and Stokes 2000, Tongway and Hindley 2000, Stringham et al. 2003). Ecosystem resistance and resilience are not static and can change in relation to varying climatic conditions and dynamic ecosystem properties affected by climate, land use, and management (Scheffer et al. 2001, Scheffer and Carpenter 2003). Some aspects of resistance and resilience also are strongly controlled by ecosystem properties that are relatively stable through time. Examples of these inherent ecosystem properties include landscape position and substrate characteristics such as rock content, texture, mineralogy, horizonation, and depth (e.g., Fig. 14).

A generalized description of factors affecting the resistance and resilience of dryland ecosystems is presented in Table C1 (Appendix C). Although generalizations can be useful, detailed considerations of resistance, resilience and other aspects of system stability are most valid when the variable of interest, benchmark conditions, spatial scale, temporal scale, and disturbance characteristics are clearly specified (Grimm and Wissel 1997). Details matter – for example, effects of specific soil physical properties on plant resistance and resilience to drought may vary with drought characteristics and among species in relation to particular ecophysiological traits. One hypothesis described earlier in this report but not captured in Table C1 is that resilience is enhanced in ecosystems where different functional-response types are nested within the same functional-effect types (Walker et al. 1999, Díaz and Cabido 2001).
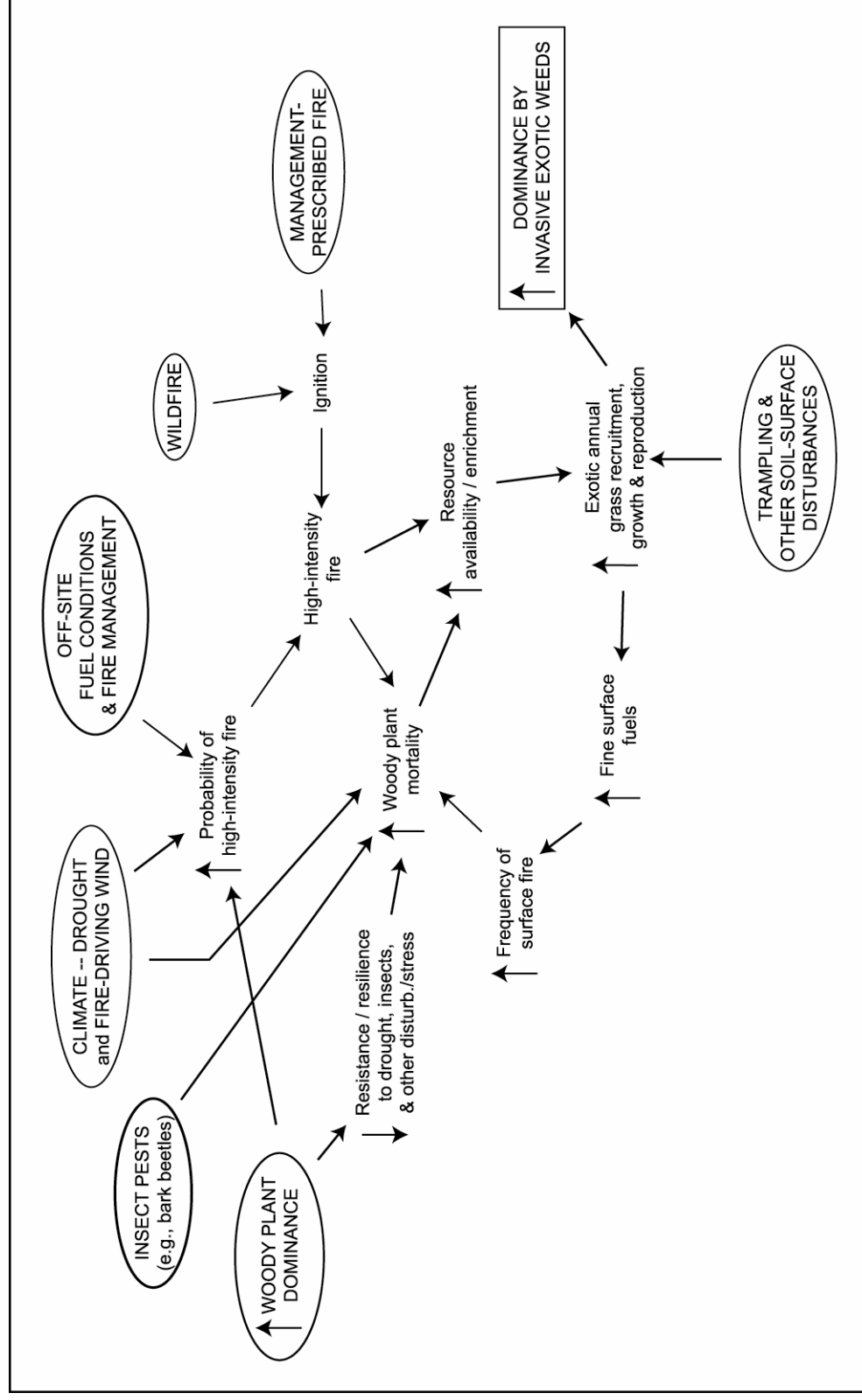
Figure 18. Conceptual model illustrating processes by which increasing woody-plant dominance, soil-surface disturbances, insect pests, climate, off-site fuel / fire conditions, wildfire, and management-prescribed fire interactively lead to increasing dominance (and site conversion) by exotic annual grasses.
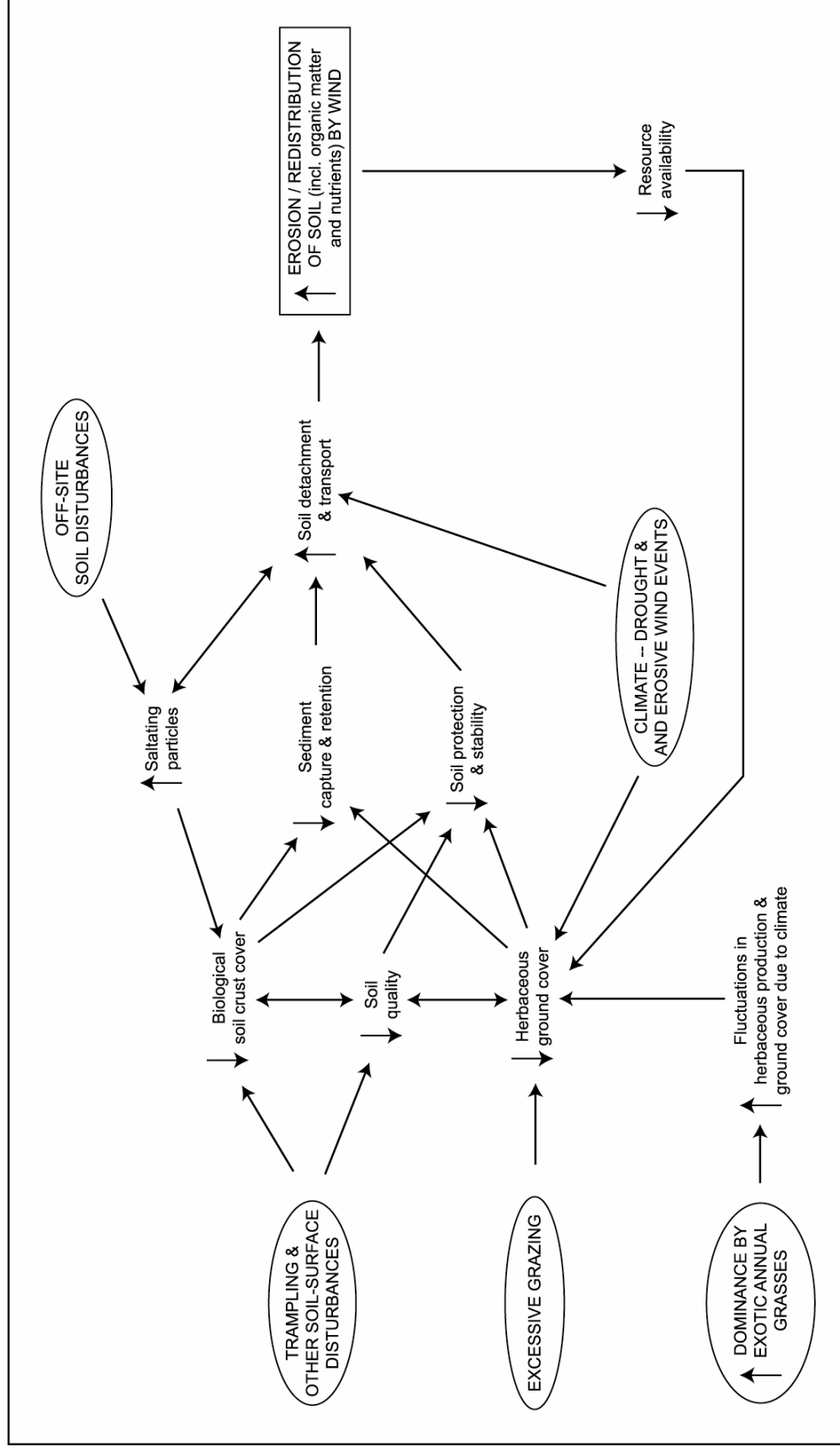
Figure 19. Conceptual model illustrating processes by which increasing site dominance by exotic annual grasses, excessive grazing, soil-surface disturbances, off-site soil-surface disturbances, and climate lead to the erosion / redistribution of soil resources by wind.
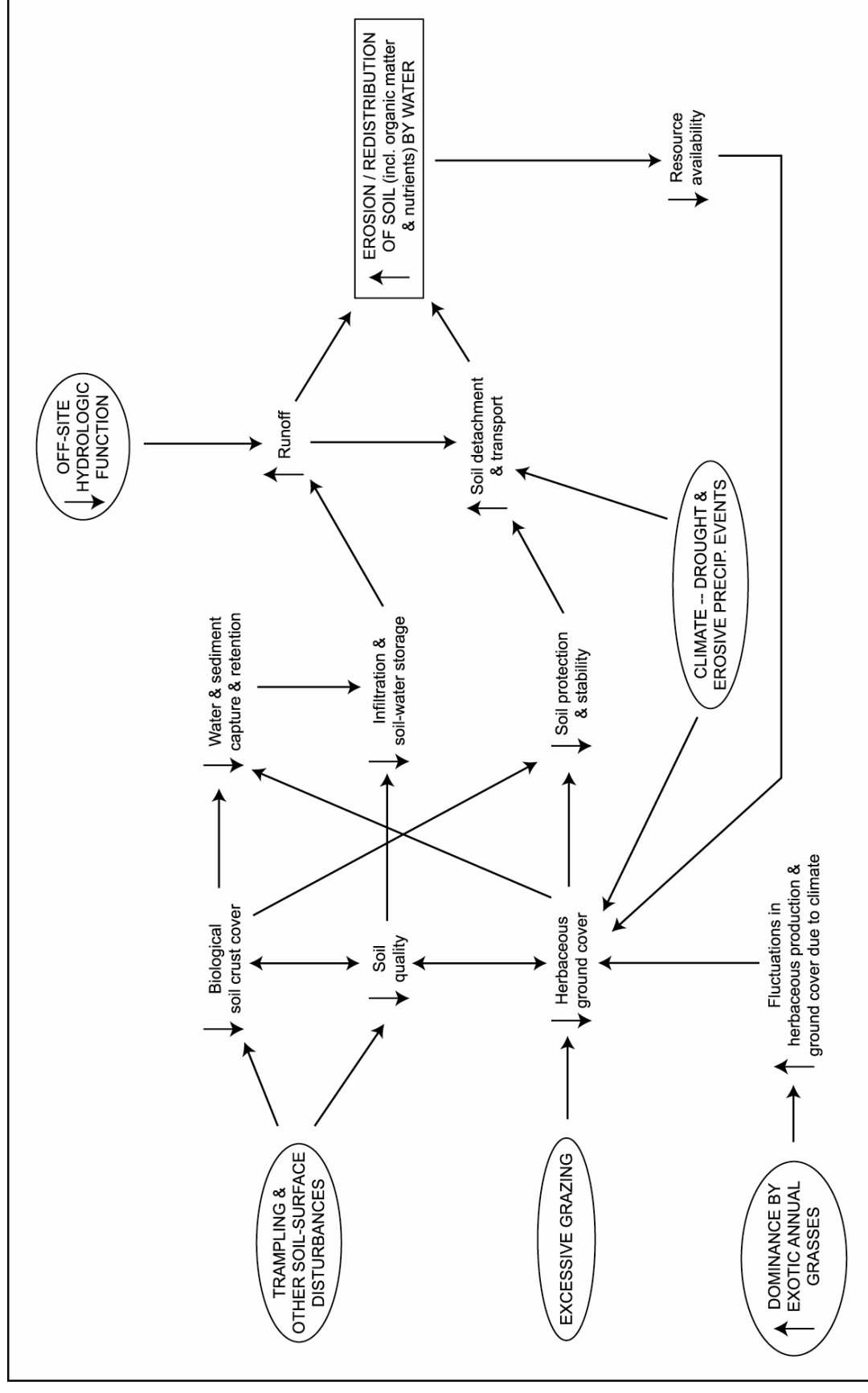
Figure 20. Conceptual model illustrating processes by which increasing site dominance by exotic annual grasses, grazing, soil-surface disturbances, off-site hydrologic dysfunction, and climate lead to the erosion / redistribution of soil resources by water.

Figure 21. Example of an annualized ecosystem at Arches National Park where climate-driven fluctuations in ground cover and persistent soil instability contribute to accelerated rates of wind erosion.

3. Implications for Ecosystem Classification

Given the importance of ecosystem resistance and resilience in affecting probabilities of ecosystem change beyond the desired range of conditions, an ideal ecosystem classification system to support ecosystem management would be based on stable properties that influence ecosystem resistance and resilience. From the preceding discussion and Table C1, general factors that most strongly affect resistance and resilience are climatic conditions, soil structure, vegetation structure, and inherent ecosystem properties described by substrate characteristics and landscape setting. Although climatic conditions themselves are not stable, latitude, elevation and aspect are three invariant factors that are certain to affect climatic conditions irrespective of the future trajectory of global climate change. To support ecosystem management and monitoring, it is therefore recommended that ecosystems be classified in relation to invariant climatic zones, substrate characteristics, and landscape setting.

For dryland ecosystems, the most widely used classification scheme based on general climatic zones and inherent site properties is the *ecological site* system of the U.S. Department of Agriculture Natural Resources Conservation Service. In this classification system, an *ecological site* is defined as a kind of land with specific physical characteristics which differs from other kinds of land in its ability to produce distinctive kinds and amounts of vegetation and in its response to management (Society for Range Management Task Group on Unity in Concepts and Terminology 1995:279).

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V. APPENDICES

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Appendix A. Primary Functions and Attributes / Measures Associated with Components of Dryland Ecosystems

Table A1. Primary functions and attributes/measures associated with components of dryland ecosystems. Components are organized in relation to the four interactive controls of ecosystem structure and function.

INTERACTIVE CONTROLS*	COMPONENTS		PRIMARY ECOSYSTEM FUNCTIONS	ATTRIBUTES / MEASURES
	Precipitation		Water inputs; drives water-limited ecosystem and population processes (e.g., nutrient cycling, C and N fixation, seed germination); erosive force for detachment, entrainment, and overland redistribution and export of soil, litter, and propagules; drives fire disturbances due to effects of interannual variability on fuel production and flammability; strongly affects ecosystem resistance and resilience to natural disturbances and anthropogenic stressors.	Seasonality; quantity; intensity (amt. per event and per unit time), duration, temporal frequency; temporal variability (among seasons, within seasons, among years), spatial variability, form (rain vs. snow), Frequency, intensity and duration of erosion-driving events.
Regional climatic and atmospheric conditions	Wind		Drives the redistribution and export (transfer among patches and among systems) of soil, litter, and propagules; affects ecosystem-atmosphere gas-exchange (CO_2 intake and evapotranspiration); energy-balance modification (transfer of sensible and latent heat).	Average sustained and peak velocities and direction (and frequency-magnitude distributions of these by season), seasonal and diurnal variability, spatial variability. Frequency, intensity and duration of erosion-driving events.
	Radiant energy		Energy inputs for photosynthesis and sensible heat; effects on ecosystem-atmosphere gas-exchange (CO_2 uptake and evapotranspiration) and energy balance. Interacts with precipitation to affect resource availability and drive biotic processes through effects on timing and rate of metabolic activity.	Maximum, minimum, and average values by season (heat), spectral characteristics, intensity; temporal variability (seasonal and diurnal), spatial variability (horizontally and vertically).
	N_2 and CO_2		Nitrogen and carbon inputs (gaseous)	Atmospheric concentration
	Dust & other airborne constituents		Mineral nutrient inputs.	Quantity, chemical composition, temporal distribution (seasonality), spatial distribution.
Disturbance regime	Episodic climatic events	Drought	Drives change in ecosystem structure and function (1) by altering competitive relations and inducing selective, potentially widespread, mortality – resulting in persistent dominance shifts among vegetative functional groups; and (2) by affecting ecosystem resistance / resilience to other natural disturbances (e.g., extreme precipitation events, wind storms, insect outbreaks, and/or fire) and anthropogenic stressors.	Seasonality, intensity, duration, frequency, extent, timing in relation to extreme precip. and wind events.
		Extreme precipitation events / floods	Drives change in ecosystem structure and function (1) by inducing selective establishment episodes (or less commonly, selective mortality) of vegetative functional groups – resulting in persistent dominance shifts; and (2) due to extreme erosive forces for detachment, entrainment, and redistribution and export of soil and soil resources, potentially inducing geomorphic change.	Seasonality, intensity, duration, frequency, timing in relation to drought and the amount of time required for biotic and biotically structured ecosystem components and functions to recover from drought.
		Wind storms	Drives change in ecosystem structure and function due to extreme erosive forces for detachment, entrainment, and redistribution and export of soil and soil resources.	Seasonality, intensity, duration, frequency, timing in relation to drought and the amount of time required for biotic and biotically structured ecosystem components and functions to recover from drought.
		Extreme temperature events	Drives change in ecosystem structure and function by inducing selective mortality, potentially resulting in long-term shifts in dominants.	Intensity, duration, frequency, extent; timing in relation to other disturbances.

Table A1 continued.

INTERACTIVE CONTROLS*	COMPONENTS	PRIMARY ECOSYSTEM FUNCTIONS	ATTRIBUTES / MEASURES
	Fire	Drives change in ecosystem structure and function (1) by directly altering vegetation structure (differential resistance and resilience to fire), including spatial heterogeneity, (2) by altering the forms, bioavailability, and spatiotemporal distribution of soil resources, and (3) by increasing runoff and soil erosion. Over longer time scales, fire may decrease erosion and runoff due to increases in herbaceous ground cover.	Intensity, spatial extent and pattern, frequency, timing in relation to other disturbances such as extreme precipitation and wind events.
	Insect / disease outbreaks	Drives change in ecosystem structure and function by inducing selective and often-widespread mortality, potentially resulting in long-term shifts among dominant functional groups. May reduce ecosystem resistance / resilience to other disturbances such as fire.	Intensity, duration, frequency, extent; timing in relation to other disturbances.
Disturbance regime (continued)	Herbivory	Drives change in ecosystem structure and function by (1) altering competitive relations among palatable and unpalatable plant taxa, (2) altering vegetation resistance and resilience to drought, other disturbances, and stressors, and (3) potentially affecting primary productivity and litter deposition. In combination, these can alter functional group structure, including spatial heterogeneity, and ecosystem capacity to capture and retain soil resources. Excretion further alters the spatiotemporal distribution of resources.	Intensity, selectivity, spatial extent and pattern, frequency, timing in relation to other disturbances such as drought and the amount of time required for biotic and biotically structured ecosystem components and functions to recover from drought.
	Digging / burrowing	Alters soil structure and function (creation of macropores potentially increase water capture and retention), alters spatiotemporal distribution of soil resources, generates patch structure / heterogeneity, potentially alters structure of vegetative functional groups due to resource alteration and creation of establishment opportunities.	Spatial distribution and extent, frequency, depth, timing in relation to other disturbances such as extreme wind and precipitation events.
	Trampling	Destabilizes soil and decreases resistance of soil to erosion and redistribution by wind and water; compacts soil (alters soil structure and function), alters structure and function of biological soil crusts; alters vegetation structure directly due to trampling of vegetation and indirectly due to effects on soil characteristics.	Intensity, spatial extent and pattern, frequency, timing in relation to other disturbances such as extreme wind and precipitation events, drought, and the amount of time required for biotic and biotically structured ecosystem components and functions to recover from drought.
	Predators	Regulation of (or response to) prey populations, including granivores and herbivores. May also impact ecosystem structure and function by digging / burrowing (see above).	Composition, quantity, population structure and dynamics; physiological condition.
Biotic functional groups	Herbivores	See Herbivory, above. May also impact ecosystem structure and function by digging / burrowing (see above). [Potential agents of disturbance – see herbivory, above.]	Composition, quantity, population structure and dynamics; physiological condition.
	Granivores	Alteration of vegetation structure (composition and spatial heterogeneity) due to selective collection, consumption, burial, and redistribution of propagules. May also impact ecosystem structure and function by digging / burrowing (see above).	Composition, quantity, population structure and dynamics; physiological condition.

Table A1 continued.

INTERACTIVE CONTROLS*	COMPONENTS	PRIMARY ECOSYSTEM FUNCTIONS	ATTRIBUTES / MEASURES
Biotic functional groups (continued)	VEGETATION: Small trees Shrubs Dwarf shrubs Perennial grasses	Energy capture and conversion, biomass production, litter deposition (soil protection and inputs to nutrient cycles), nutrient retention (intraplant cycling), environmental modification (reducing soil temperatures and evaporative rates via shading and litter deposition; generating resource heterogeneity via uptake, litter deposition, and capture of waterborne and windborne materials), obstruction to wind and overland water flow (reducing erosive energy and enhancing capture and retention of soil resources), rainfall interception and redistribution via stemflow (reducing erosive energy and enhancing capture and retention of soil resources). In combination, these functions contribute to resistance / resilience of soil functions to disturbance by trampling and erosive forces of wind and water. Provide fuel for fire and habitat structure for vertebrates and invertebrates.	Composition, quantity (cover and biomass), population structure and dynamics, vertical structure, spatial distribution / heterogeneity, photosynthetic pathway, leaf longevity, litter quantity and quality (e.g., C:N), flammability, productivity; physiological activity and condition; resistance & resilience of structure and function to dominant natural disturbances and anthropogenic stressors.
	Biological soil crusts (photoautotrophs)	Soil stabilization and soil-surface protection; energy capture and conversion; nutrient capture, retention, and cycling (N fixation, capture of airborne minerals in dust); obstruction to overland water flow (increased surface roughness enhances capture and retention of soil resources); environmental modification (albedo & soil temperature,); soil-temperature increases (decreased albedo); habitat creation (due to long-term soil stabilization).	Composition, quantity (cover and biomass), spatial distribution and contiguity, microtopographic heterogeneity / surface roughness; physiological activity and condition; productivity; resistance & resilience of structure and function to dominant natural disturbances and anthropogenic stressors.
The Soil Surface			
The Soil Continuum — Roots	Roots	Soil stabilization, nutrient and water acquisition and transport, water redistribution in soil profile, organic-matter inputs (exudates & tissues), macropore creation, rhizosphere acidification (release CO_2 and organic acids).	Morphology, density, horizontal and vertical distribution, spatial and temporal patterns of physiological activity, productivity.
	Soil biota (heterotrophs)	Litter decomposition and nutrient cycling, N fixation, symbiotic relations with vascular plants (symbiotic enhancement of nutrient and water delivery to vascular plants may increase resistance / resilience of these plants to drought or other disturbances).	Composition, quantity (biomass), spatial distribution vertically and horizontally, temporal distribution, spatial and temporal patterns of physiological activity; productivity; resistance & resilience of structure and function to dominant natural disturbances and anthropogenic stressors.
	Soil mineral matrix Soil organic matter Soil water Soil air	Nutrient storage, supply, and cycling; water storage and supply; medium for plant growth; habitat for soil biota involved in nutrient cycling; positive effects on resistance / resilience of vegetative functional groups to drought, herbivory, and trampling.	Inherent properties (relatively insensitive to change): Mineralogy and texture by depth, spatial heterogeneity in these properties, depth. Dynamic properties (subject to change): Aggregate stability and bulk density (structure), organic-matter quantity and quality (e.g., C:N), depth (often considered an inherent property, but subject to change over decadal time scales), erosion rate, infiltration rate, biotic activity, surface crusting (biotic or physicochemical), surface roughness, spatial heterogeneity of these properties, resistance & resilience of structure and function to dominant natural disturbances and anthropogenic stressors.
Soil resources	Soil temperature	Regulates physiological activity of autotrophic and heterotrophic soil biota, including roots.	Maximum, minimum, and average values by season; temporal variability (seasonal and diurnal), spatial variability (horizontally and vertically).

Primary sources: Whitford (2002), Herrick et al. (2002), Belnap and Lange (2001), Ehleringer et al. (2000), Seybold et al. (1999), Whisenant (1999), and Ludwig et al. (1997).
* Interactive controls are constrained by the five state factors—(1) global/regional atmospheric resources and conditions, (2) topography, (3) parent material, (4) potential biota, and (5) time (Jenny 1980, Chapin et al. 1996).

Appendix B. Potential Ecological Effects of Major Anthropogenic Stressors

Table B1. Potential effects of major anthropogenic stressors on structure and functioning of dryland ecosystems. Potential impacts of changing temperatures, atmospheric chemistry, and atmospheric circulation patterns (including precipitation) are excluded.

Stressors	Stress mechanisms	Potential effects on ecosystem components and functions (emphasizing effects on energy flow, nutrient capture and retention, water capture and retention)
Park use by terrestrial recreationists	Trampling of soil and vegetation	Damaged biological soil crusts and vascular plants, decreased N fixation by biological crusts, decreased soil-surface roughness, enhanced recruitment opportunities for exotic plants favored by soil destabilization, altered vegetation structure, decreased soil protection by biological crusts, decreased soil aggregate stability, decreased soil stability, decreased resistance of soil to erosion by wind and water, increased bulk density, decreased infiltration, increased overland flow of water, decreased soil-water availability for plant growth, soil biotic activity, and nutrient cycling; decreased root growth and soil-organic-matter inputs, decreased plant growth, decreased resistance and resilience of plants to drought, increased redistribution and export of soil, litter, nutrients, and water; decreased capacity of ecosystem to capture and retain soil resources; multiple cascading effects due to feedbacks among soil functions, soil-resource retention, resource heterogeneity, and vegetation structure.
	Introduction of invasive exotic plants	See exotics, below.
Livestock & other large herbivores	Trampling of soil and vegetation	See trampling, above.
	Excessive herbivory	Altered competitive relations of plants, reduced plant canopy cover, reduced fine fuels and frequency of of low-intensity surface fires, altered vegetation structure (e.g., dominance shift from palatable plants to unpalatable plants, or from herbaceous plants favored by fire to woody plants eliminated by fire), reduced plant-canopy protection of soil, reduced vegetative obstruction of wind and overland water flow, reduced capture and retention of soil resources, reduced litter deposition and litter-protection of soil, reduced soil-organic-matter inputs, reduced soil aggregate stability, decreased resistance and resilience of soil to trampling, decreased root growth, decreased resistance and resilience of grazed plants to drought; multiple cascading effects due to feedbacks among vegetation structure, soil-resource retention, resource heterogeneity, and soil functions.
	Excretion	Nutrient losses (N volatilization), nutrient immobilization in dung pats, increased spatial and temporal heterogeneity of nutrients, eventual alteration of vegetation structure, facilitation of exotic-plant invasion where nutrients locally enriched (see exotics, below).
	Introduction of invasive exotic plants	See exotics, below.
Fire suppression	Altered fire regime	Decreased frequency and extent of fire, altered vegetation composition / structure (e.g., dominance shift from herbaceous plants favored by fire to woody plants eliminated by fire), increased accumulation of coarse-woody fuels, increased likelihood of high-intensity canopy fire, decreased ecosystem resistance / resilience to impacts from drought and insect outbreaks
Invasive exotic plants	Competition with native plants	Altered vegetation composition / structure, eventual alteration of soil-resource dynamics and/or heterogeneity due to vegetation-soil feedbacks.
	Altered soil-resource dynamics	Altered nutrient dynamics (e.g., exotic characterized by different tissue chemistry, and/or by different spatiotemporal patterns of nutrient uptake and litter deposition than native plants), altered soil-water dynamics (e.g., exotic characterized by different spatiotemporal patterns of water use than native plants), eventual alteration of vegetation composition / structure due to soil-vegetation feedbacks.
	Altered disturbance regime	Increased frequency and extent of fire (facilitated by increased quantity, flammability, and/or spatial continuity of fuels); eventual alterations of vegetation composition / structure and soil-resource availability due to strong feedbacks among fire, vegetation structure, and resource availability.
	Trespass livestock	See livestock, above.
	Introduction of exotic plants	See exotics, above.
Adjacent land-use activities	Accelerated transfers of sediment, nutrients, and water	Soil-resource enrichment, eventual alteration of vegetation composition / structure, facilitation of exotic-plant invasion where resources enriched (see exotics, above), increased overland water flow (increased erosive energy of water), increased redistribution and export of soil and nutrients.
	Fire from adjacent lands	Increased susceptibility to high-intensity fire and associated ecosystem changes.
	Altered landscape structure	Altered habitat structure, connectivity and habitat-use patterns of wildlife.
Air pollutants	Nitrogen deposition	Soil-resource enrichment, potential alteration of vegetation composition and structure -- including facilitation of exotic-plant invasion (see exotics, above).
	Ozone	Altered competitive relations between ozone-sensitive and ozone-tolerant plants, altered vegetation composition & structure

Appendix C. Factors Affecting Resistance and Resilience of Dryland Ecosystems

Table C1. Climatic conditions, inherent ecosystem properties, and dynamic ecosystem properties hypothesized to confer resistance and resilience to selected ecosystem attributes in relation to particular disturbances or stressors. (BSC = biological soil crust.)

Disturbance or stressor	Ecosystem attribute	Climatic conditions		Inherent ecosystem properties[1]		Dynamic ecosystem properties[2]	
		Resistance	Resilience	Resistance	Resilience	Resistance	Resilience
Drought	Native grass population structure		Antecedent moisture & temperature conditions favorable for seed production by native plants; Subsequent moisture & temperature conditions favorable for plant growth & soil biotic activity; precipitation characterized by timing, intensity and event size that maximize likelihood of infiltration and soil-water recharge	Deep sandy soil; run-on landscape position		Soil and vegetation structure that enhance site capacity to capture, retain and cycle water and mineral nutrients; physiological condition of native grass populations unimpacted by other disturbances or stressors (e.g., excessive herbivory)	Seed / propagule banks; soil and vegetation structure that enhance site capacity to capture, retain and cycle water and mineral nutrients; physiological condition of native plant populations unimpacted by other disturbances or stressors; absence of invasive exotic species capable of rapid population expansion and exclusion of native plant populations
	Shrub / tree population structure	Coincident temperatures and winds that do not exacerbate evaporational demands		Rocky soil (including rock outcrops with joints and fractures); run-on landscape position		Natural stand structure (i.e., not overstocked); soil and vegetation structure that enhance site capacity to capture, retain and cycle water and mineral nutrients; physiological condition of native shrub-tree populations unimpacted by other disturbances or stressors	
Insect outbreak (here assumed to be triggered by drought stress)	Tree population structure	Antecedent and coincident moisture & temperature conditions favorable for tree growth	Antecedent moisture & temperature conditions favorable for seed production by native plants; Subsequent moisture & temperature conditions favorable for tree growth	Rocky soil (including rock outcrops with joints and fractures); run-on landscape position		Natural stand structure (i.e., not overstocked); soil and vegetation structure that enhance site capacity to capture, retain and cycle water and mineral nutrients; physiological condition of native shrub-tree populations unimpacted by other disturbances or stressors	Seed / propagule banks; soil and vegetation structure that enhance site capacity to capture, retain and cycle water and mineral nutrients; physiological condition of native plant populations unimpacted by other disturbances or stressors; absence of invasive exotic species capable of rapid population expansion and exclusion of native plant populations

[1] Inherent ecosystem properties are relatively insensitive to change in relation to land use, management and climate (e.g., soil texture, mineralogy, horizonation, depth; landcape/topographic position).

[2] Dynamic ecosystem properties are sensitive to change in relation to land use, management and climate (e.g., soil structure and biotic activity; vegetation composition and structure). Dynamic properties are generally mediated by biotic processes.

Table C1 continued.

Disturbance or stressor	Ecosystem attribute	Climatic conditions		Inherent ecosystem properties		Dynamic ecosystem properties	
		Resistance	Resilience	Resistance	Resilience	Resistance	Resilience
Surface fire (as natural disturbance)	Native vegetation composition & structure	Antecedent moisture & temperature conditions that diminish fuel production and/or diminish fuel flammability; calm wind conditions	Subsequent moisture & temperature conditions favorable for plant growth & soil biotic activity	Natural landscape fragmentation (i.e., sites potentially capable of supporting surface fire are discontinuously distributed in the landscape, separated by natural fuel breaks)	--	Abundance and spatial continuity of fine surface fuels inadequate to carry fire	Seed / propagule banks; soil and vegetation structure that enhance site capacity to capture, retain and cycle water and mineral nutrients; physiological condition of native plant populations unimpacted by other disturbances or stressors; absence of invasive exotic species capable of rapid population expansion and exclusion of native plant populations through competition or alteration of fire regimes
Stand-replacing canopy fire (as natural disturbance)	Native vegetation composition & structure	Antecedent moisture & temperature conditions that diminish fuel production and/or diminish fuel flammability; calm wind conditions	Antecedent moisture & temperature conditions favorable for seed production by native plants. Subsequent moisture & temperature conditions favorable for vegetative reproduction (for sprouters), plant establishment, plant growth & soil biotic activity	Natural landscape fragmentation (i.e., sites potentially capable of supporting high-intensity stand-replacing fire are discontinuously distributed in the landscape, separated by natural fuel breaks)	--	Abundance and spatial continuity of ladder and canopy fuels inadequate to carry fire	Seed / propagule banks; soil and vegetation structure that enhance site capacity to capture, retain and cycle water and mineral nutrients; physiological condition of native plant populations unimpacted by other disturbances or stressors; absence of invasive exotic species capable of rapid population expansion and exclusion of native plant populations through competition or alteration of fire regimes

Table C1 continued.

Disturbance or stressor	Ecosystem attribute	Climatic conditions		Inherent ecosystem properties		Dynamic ecosystem properties	
		Resistance	Resilience	Resistance	Resilience	Resistance	Resilience
Erosive wind events	Soil retention (includes fine soil particles, litter, organic matter, nutrients)	Antecedent and coincident moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, maintenance of moist soil conditions, formation of stable soil aggregates, and/or formation of physical crust	Antecedent moisture & temperature conditions favorable for seed production by native plants / Subsequent moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, maintenance of moist soil conditions, formation of stable soil aggregates, and/or formation of physical crust	Landscape setting that provides protection from erosive winds due to aspect, absence of wind-funneling landforms, minimal fetch exposure, etc.; soils with low erodibility by wind (e.g., fine-textured soil not exposed to bombardment from saltating sand particles; soil surface covered by rock fragments)	Soil physical and chemical properties and landscape setting (e.g., north-facing aspect) that favor plant growth, BSC growth, soil biotic activity, and/or reformation of physical crust	Soil aggregate stability and ground cover of BSCs, stable litter, and/or other soil-stabilizing features at maximum levels relative to potential (i.e., undiminished by other disturbances or stressors); vegetation structure that obstructs wind and reduces near-surface wind velocity (e.g., tall, closely spaced vegetation)	Seed / propagule banks; unconstrained BSC growth, plant growth, litter accumulation, soil biotic activity, and soil aggregation; soil and vegetation structure that enhance site capacity to capture, retain and cycle water and mineral nutrients
Erosive precipitation / flood events	Soil & water retention (includes fine soil particles, litter, organic matter, nutrients)	Antecedent moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, and formation of stable soil aggregates / Coincident moisture & temperature conditions favorable for maintaining soils in moist or frozen state (frozen or dry in case of clay soils)	Antecedent moisture & temperature conditions favorable for seed production by native plants / Subsequent moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, and formation of stable soil aggregates	Deep sandy soil (high infiltration and storage capacity); soil surface covered by rock fragments; low slope gradient; short slope length; landscape position that does not receive run-off from upslope positions	Soil physical and chemical properties and landscape setting (e.g., north-facing aspect) that favor plant growth, BSC growth, and soil biotic activity	Soil aggregate stability and ground cover of BSCs, stable litter, and/or other soil-stabilizing features at maximum level relative to potential (i.e., undiminished by other disturbances or stressors); vegetation structure that obstructs over-land water flow, increases flow tortuosity, and reduces flow velocity	Seed / propagule banks; unconstrained BSC growth, plant growth, litter accumulation, soil biotic activity, and soil aggregation; soil and vegetation structure that enhance site capacity to capture, retain and cycle water and mineral nutrients
Trampling & other soil-surface disturbances	Soil stability (susceptibility to wind erosion)	Antecedent moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, and formation of stable soil aggregates.	Antecedent moisture & temperature conditions favorable for seed production by native plants / Subsequent moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, formation of stable soil aggregates, and/or formation of physical crust	Soil surface covered by rock or rock fragments	Soil physical and chemical properties and landscape setting (e.g., north-facing aspect) that favor plant growth, BSC growth, soil biotic activity, or reformation of physical crust	Maximum degree of soil stabilization provided by biotic features relatively unimpacted by trampling or other soil-surface disturbances, such as stable litter, continuous herbaceous ground cover, and continuous canopy cover. Soil stability in relation to wind erosion not dependent on integrity of sensitive biological or physical crusts.	Seed / propagule banks; unconstrained BSC growth, plant growth, litter accumulation, soil biotic activity, and soil aggregation; soil and vegetation structure that enhance site capacity to capture, retain and cycle water and mineral nutrients

Table C1 continued.

Disturbance or stressor	Ecosystem attribute	Climatic conditions		Inherent ecosystem properties		Dynamic ecosystem properties	
		Resistance	Resilience	Resistance	Resilience	Resistance	Resilience
Trampling & other soil-surface disturbances	Soil stability and infiltration capacity (susceptibility to water erosion)	Antecedent moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, and formation of stable soil aggregates. Coincident conditions: in presence of BSCs, moist or frozen soils; in absence of BSCs, frozen or dry soils.	Antecedent moisture & temperature conditions favorable for seed production by native plants. Subsequent moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, and formation of stable soil aggregates. Occurrence of wet-dry or freeze-thaw cycles required to enhance recovery of compacted soils.	Sandy soil, or soil surface covered by rock or rock fragments. Soil physical and chemical properties and landscape setting (e.g., north-facing aspect) that favor plant growth, BSC growth, and soil biotic activity		Maximum degree of soil stabilization provided by biotic features relatively unimpacted by trampling or other soil-surface disturbances, such as stable litter, continuous herbaceous ground cover, and continuous canopy cover. Site hydrologic functioning and soil stability in relation to water erosion not dependent on integrity of sensitive BSCs.	Seed / propagule banks; unconstrained BSC growth, plant growth, litter accumulation, soil biotic activity, and soil aggregation; soil and vegetation structure that enhance site capacity to capture, retain and cycle water and mineral nutrients
Excessive herbivory	Native vegetation structure & composition	Antecedent and coincident moisture & temperature conditions favorable for plant growth and soil biotic activity	Antecedent moisture & temperature conditions favorable for seed production by preferred forage species. Subsequent moisture & temperature conditions favorable for soil biotic activity and regrowth, seed production, and germination / establishment of defoliated plants	Soil physical and chemical properties and landscape settings that DO NOT favor growth of plants that are palatable to predominant large-bodied herbivores. Soil physical and landscape settings that DO NOT facilitate access or mobility of predominant large-bodied herbivores	Soil physical and chemical properties and landscape setting (e.g., rich alluvial soils, riparian corridors) that favor vigorous plant growth and soil biotic activity	Plant communities with no plant species palatable to predominant large-bodied herbivores OR Plant communities in which all species are equally preferred by predominant large-bodied herbivores and exhibit similar physiological / morphological responses to defoliation (i.e., preferential herbivory does not favor one species over another)	Seed / propagule banks; soil and vegetation structure that enhance site capacity to capture, retain and cycle water and mineral nutrients; physiological condition of defoliated plant populations unimpacted by other disturbances or stressors; absence of unpalatable plants (woody or herbaceous, native or exotic) capable of rapid population expansion and exclusion of palatable native plant populations through competition or alteration of fire regimes
Invasive exotic plants	Native vegetation structure & composition	Conditions that favor native plant communities relative to invaders (will vary among communities and invaders); in general, conditions that constrain resource availability		Soil physical and chemical properties and landscape settings that present harsh resource constraints for vascular plants	--	Growth, competitive ability, and reprod. of native plant populations undiminished by other disturbances or stressors; soil-surface conditions that restrict safe-site opportunities for invasives	Growth, competitive ability, and reproduction of native plant populations undiminished by other disturbances or stressors